IMPERIAL INSTITUTE
OF
AGRICULTURAL RESEARCH, PUSA.

THE QUARTERLY REVIEW *of* BIOLOGY

VOLUME IV
1929

Published by
THE WILLIAMS & WILKINS COMPANY
BALTIMORE
U. S. A.

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THE QUARTERLY REVIEW *of* BIOLOGY

BIOMETRICAL STUDIES ON VARIATION AND RACES OF THE HONEY BEE (APIS MELLIFERA L.)

BY W. W. ALPATOV

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INTRODUCTION

THE purpose of the present paper is to bring together in a systematized form numerous data on the variation of the honey bee accumulated during the last five years, mostly by Russian investigators. Although the insects have been for years among the favorite objects for the discussion of variation little has been done with them along exact biometrical lines.

The honey bee may be considered an insect whose biometry is at the present moment better known than that of any of the others, and may be compared with *Drosophila*, the best known animal from the genetical point of view. G. A. Koshevnikov (33) was the first zoologist who introduced exact measurement of different parts of the exoskeleton of the honey bee as a method of study. From a statistical point of view this attempt was very incomplete because of the restricted number of observations made by this investigator. To a similar category must be referred many attempts to study the variation of the honey bee tongue, published during 1900 and 1901 in the leading American beekeeping magazines like *Gleanings in Bee Culture*. Other early articles such as those of Kulagin (35) and Martynov (38) belong to the same group of inexact papers on variation problems in the honey bee.

At this pioneer period of work in the variation of the honey bee the development of biometry in general was not high enough, and the appreciation of the biologists was also not keen enough for it to prove a useful tool in the field of variation of the honey bee. The article of Chochlov (22), a student of Professor Koshevnikov, can be considered as a new step toward the solution of our problem. This author started to measure considerable numbers of bees and to calculate biometrical constants. His measurements of the bee tongue include 1899 individuals belonging to six races, each race being represented by three colonies. The interpretation of the biometrical constants, given without sufficient experience, challenged Philiptschenko (66) to devote a special paper to the recalculation and discussion of Chochlov's data. The conclusions of both of these authors are that different bee races have specific average tongue lengths. A. S. Michailov (39) compared Chochlov's data with his own measurements of three hundred bees from Tcherepowetz, North Russia, and the measurements obtained by him from the Tula Apicultural Station. He pointed out that the tongue length of bees in the plain of European Russia changes from the north to the south, showing a regular increase in the south. Michailov's publication stimulated the author of the present paper to work out statistically all the measurements available at that time (3).

In the year 1924 the author of the present article began on a very large scale to collect bees from all parts of Russia and Caucasus. Several Russian apicultural experimental stations like Tula, Kasan, and Kharkov, as well as private investigators, turned over their numerous measurements for biometrical computations. The work of the author of this article was closely connected with the Zoological Museum of the University of Moscow (Director, Prof. G. A. Koshevnikov) and was financed by the Bureau of Experimental Stations of the Russian Department of Agriculture. At the conference of the Russian Apicultural Experimental Stations held in Moscow in 1925, a special agreement was established concerning the distribution of problems among the apicultural research institutions in Russia. The Zoological Museum took over the problems of geographical variation, and the Tula Experimental Station, with which A. S. Michailov has been affiliated since 1925, worked out a very elaborate plan of investigation of the influence of different factors on the variation of the honey bees of a given apiary. Numerous papers of Michailov and of the author published since 1924 will be discussed in systematized form later on. Thanks to the obtaining of a research fellowship from the International Education Board, the author had the opportunity to come over to the United States of America. The whole summer of 1927 was spent in the hospitable laboratory of Professor Phillips at Cornell University. His kind help in procuring the necessary material made it possible to work out the variation of the races of the honey bee cultivated in the United States. The final calculations and preparation of the manuscript were done under Dr. Raymond Pearl, to whom we are deeply indebted for many valuable suggestions and criticisms.

COLONY VARIATION AS A BASIS FOR RACIAL STUDIES IN SOCIAL INSECTS

One of the most important facts which must be born in mind in every biometrical investigation on animals living in colonies is the family variation, that is, the differences between the characteristics of the colonies. It has been shown by several investigators, Thomson, Bell and Pearson (76, 77), Warren (79), Arnoldi (17), and Palenitschko (62) that in different groups of social insects the variation of single families is smaller than the variation of the whole population. Table 1 shows that the arithmetical means of single families differ considerably. The same can be seen in Figure 1, where variation curves of six of these Kharkov colonies are represented. If we sum up the coefficients of variation of all the colonies and divide the sum by the number of colonies we shall get a constant showing the average variation of the colony. In the case of the Kharkov apiary it will be equal to 1.56, while the coefficient of variation for the frequency distribution representing all 800 bees is equal to 1.95, as can be seen from Table 1. Hence, expressing 1.56 in per cent of 1.95 we get 80 per cent. That is, we can say that the mean variability of the colony is equal to 80 per cent of the total variability of the apiary. We have calculated the expression of colony variation in per cent of the variation of the apiary for different apiaries. The results are represented in Table 2.

TABLE 1

Means and coefficients of variation of the tongue length of eight colonies of the apiary of the Kharkov Apicultural Experimental Station. One hundred bees have been measured from each colony

(From Alpatov, 1927)

Mean in mm.........	6.423±.007	6.501±.009	6.506±.006	6.541±.007	6.544±.008	6.598±.005	6.608±.007	6.667±.007	6.549±.003
Coefficient of variation	1.68 ±.08	2.06 ±.10	1.30 ±.06	1.52 ±.07	1.72 ±.08	1.22 ±.06	1.47 ±.07	1.53 ±.07	1.95 ±.03
Number of the colony	20	1	3	21	9	7	2	8	All bees together

TABLE 2

Average colony coefficients of variation expressed in per cent of the coefficients of variation of the whole apiary

LOCALITY	AVERAGE VARIABILITY OF A COLONY	VARIABILITY OF THE WHOLE APIARY	PER CENT
Kasan Apicultural Experimental Station........................	1.78	2.53±.04	70.3
Moscow Apicultural Experimental Station.....................	2.01	2.13±.03	94.8
Tula Apicultural Experimental Station........................	1.50	2.04±.02	73.5
Kharkow Apicultural Experimental Station....................	1.56	1.95±.03	80.0
Nizhni Nowgorod Zootechnical Station........................	1.91	2.37±.03	80.6
Jaroslawl District (private apiaries)...........................	1.59	1.87±.03	85.0
Perm University Farm Apiary..................................	1.75	1.83±.02	95.6

The ratios for the Moscow and Perm bees stand apart, showing the great homogeneity of the bees of these apiaries. In regard to the peculiarity just described the honey bee has analogies in other groups of animals which have been studied from the point of view of variability of families. The most exact investigations on family variation are those of J. Schmidt, who did extensive work on a North Atlantic viviparous fish *Zoarces viviparus* L. (71). It has been shown by this author that the differences between families are hereditary. The same conclusion as to the hereditary origins of family differences can be drawn from the observation of Miss T. Dementiewa (24), who has bred the offspring of single females of the fresh water crustacean *Cyclops strenuus* Fisch. under uniform conditions as far as possible. Judging by analogy it may be supposed that in the colony differences of bees, heredity plays an important rôle. On the other hand one must bear in mind that in the bee as well as in other animals the conditions of development (temperature, food, size of cells and so forth) have a certain influence on the organism. In a recently published article Michailov (55) has shown that brood of the same origin developed in two colonies differing in their average tongue length develops into adult bees approximating in tongue length to their nurse colonies. His data in recalculated form are shown in Table 3.

It is interesting to note that in the honey bee the relation of the average

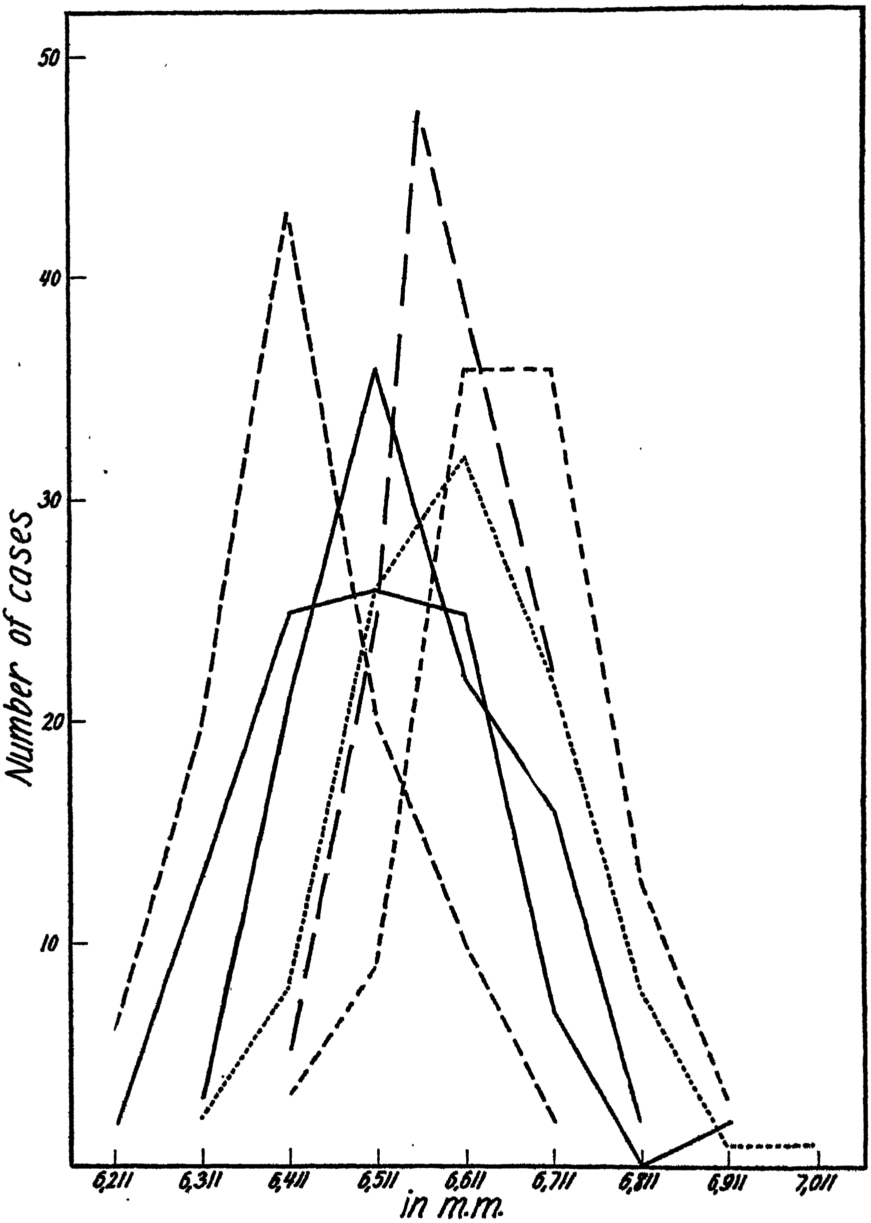

Fig. 1. Variation Curves of the Tongue Length of Six Colonies from the Kharkov Experimental Apicultural Station

Vertical axis represents the actual number of individuals. (Based on data published by Alpatov, 1927.)

colony variation to the apiary variation is expressed by comparatively very high values of the ratio (70–95 per cent). For other animals the values are much lower: for *Aphis*, 60 per cent (Warren, 78); for *Zoarces*, 56 per cent (Schmidt); for

Vespa vulgaris, 49.6 per cent (Pearson and others); for *Termes*, 43 per cent (Warren); and 72–91 per cent for different measurements in *Cyclops* (Dementiewa). It seems to us that the most probable explanation of the difference in the value of the percentage expression of individual and racial variation between the honey bee and almost all wild animals (except *Cyclops*) is that in the honey bee we compare the variation of a family with the variation of a comparatively limited group of individuals representing the population—bees belonging to one apiary and very likely connected with each other by different degrees of blood relationship. In the case of wild animals we compare the variation of the family with the variation of the whole race. The hereditary homogeneity of an apiary depends a great deal upon the hereditary relationship of the queens of the apiary. If the apiary contains many swarms obtained by inbreeding within narrow limits the colonies will be very much alike, and the colony variability will be reduced. At the present moment, with no adequate knowledge of the heredity of quantitative characters in bees, we can only make hypotheses about the comparative importance of internal and external conditions which produce the observed differences among colonies.

TABLE 3

Physical characteristics of bees developed in the maternal colony and of bees developed from eggs transferred to another colony. One hunded bees in each sample

(Recalculated from Michailov, 1928)

ORIGIN OF THE EGGS	EGGS OF THE QUEEN OF THE COLONY N 112				EGGS OF THE QUEEN OF THE COLONY N 5			
Place of development	Developed in the colony N 112		Put for development into colony N 5		Developed in the colony N 5		Put for development into colony N 112	
	Mean	Coefficient of variation	Mean	Coefficient of variation	Mean	Coefficient of variation	Mean	Coefficient of variation
Tongue.....	6.233±.007	1.67±.08	6.112±.007	1.65±.08	6.088±.006	1.50±.07	6.141±.005	1.32±.06
Length of the wing.	9.250±.010	1.57±.07	9.107±.008	1.35±.06	9.080±.008	1.36±.06	9.201±.008	1.35±.06
Width of the wing.	3.107±.004	1.76±.08	3.039±.004	1.84±.09	3.088±.004	1.98±.09	3.129±.004	1.99±.09
Third and fourth tergum...	4.704±.006	2.03±.10	4.617±.006	1.84±.09	4.658±.006	1.94±.09	4.690±.006	1.88±.09
Number of hooks....	21.41±.11	7.85±.37	21.51±.11	7.88±.38	20.59±.13	9.14±.44	20.65±.13	9.40±.45
	PROPORTIONS*							
Tongue....	132.55±.22	2.45±.12	132.42±.21	2.30±.11	130.74±.20	2.28±.10	130.98±.19	2.13±.10
Wing length	196.71±.30	2.30±.11	197.31±.27	2.05±.10	194.99±.26	2.00±.10	196.24±.28	2.09±.10
Wing width	33.59±.03	1.51±.07	33.37±.03	1.51±.07	34.01±.04	1.60±.08	34.01±.04	1.61±.08

* The explanation of the method of calculating the proportions will be given further on (p. 11).

In our paper (with F. A. Tjunin, 4) the attempt was made to show that the colonies differ from each other not only in the averages of their characteristics but also in the coefficients of correlation between the characteristics. Table 4 represents an example, in which the means of the mentum and ligula of two colonies of bees of the Tula Apicultural Experimental Station give no statistical significant differences, while the correlations of the given characters in the two colonies are quite different.

The general conclusion reached from the family variation investigations is that the family is the lowest taxonomical grouping, characterized not only by its averages but by the manner of correlation of one part of the body with another. In that regard we agree perfectly with the conclusion drawn by J. Schmidt (71): "The individual offspring analyses showed that the smallest unit hitherto considered 'race' can be resolved into still smaller elements expressed by the averages of the offspring samples. The minor elements may differ widely one from another, and also from the average of the population (race), but when taken together as a whole, they present the picture of the race, as this is expressed by our population analyses."

TABLE 4

Biometrical constants of two colonies of bees of the Tula experimental station

(From Alpatov and Tjunin, 1925)

	MEANS OF THE MENTUM IN MM.	COEFFICIENT OF CORRELATION BETWEEN MENTUM AND LIGULA	MEAN OF THE LIGULA IN MM.
Colony No. 53	1.604±.0013	0.349±.034	3.952±.0029
Colony No. 83	1.609±.0021	0.638±.029	3.957±.0033
Differences between the constants and $R = \frac{\text{Diff.}}{\text{P.E.}}$	0.005±.0025	0.289±.046	0.005±.0044
	R = 2.0	R = 6.3	R = 1.1

TABLE 5

Biometrical constants of samples of Tula bees

(From Alpatov, 1927)

	MEAN	STANDARD DEVIATION	COEFFICIENT OF VARIATION
First sample 5 bees from each colony	6.241±.014	0.152±.010	2.28±.15
Second sample 5 bees from each colony	6.231±.013	0.132±.009	2.12±.14
Two samples added together	6.236±.009	0.136±.007	2.20±.10

The just discussed colony variation among bees has a very high importance in relation to the methods of racial investigation in this form. As early as 1924 we (2) discussed the same problem in relation to the taxonomy of the ants. The conclusion was that, owing to the fact that the colony variation represents only a part of the racial variation, we must collect for investigation individuals taken not from one nest but from as many colonies as possible. The following procedure illustrates the conclusion just drawn.

We had in our possession 2500 cards with tongue lengths of bees from ten colonies of Tula bees. The cards were kept in separate envelopes, representing hives of the given apiary. From each envelope a sample of five cards was taken at random. This was repeated twice and the constants of the two distributions as well as of a combined distribution including one hundred bees were calculated. Table 5 represents the constants obtained.

Comparing the data based on these samples with the average length of Tula bee tongues calculated from the whole available material, consisting of 2500 bees, we see that the latter mean, being equal to 6.220 ± .002, differs from those in Table 5 only in the second decimal place.

Averages were next calculated taking bees belonging to groups of colonies taken at random. It was decided to take three colonies in the group, this number being used in racial investigations by Chochlov (22) and Michailov. The accompanying Table 6 shows that the constants obtained, in spite of the very large number of individuals (600–800) give a higher deviation from the true mean length of tongue of the Tula bees than did the sample of 5. The values differ in the first decimal place. This fact sets before us a very important requirement concerning the collecting of material for racial investigations on bees. The ideal condition would be to take all the individuals from different colonies, or at least to make the number of colonies not less than ten. Conclusions based on a smaller number of colonies belonging to a given race may give a completely false conclusion as to the true picture of the racial characteristics. We have tried in all our work to follow the principle just prescribed, unless the lack of material compelled us to restrict the number of colonies.

TABLE 6

Biometrical constants of samples of Tula bees, three colonies in a sample

(From Alpatov, 1927)

NUMBER OF THE COLONIES	NUMBER OF INDIVIDUALS	MEAN	STANDARD DEVIATION	COEFFICIENT OF VARIATION
10 44 83	600	6.191±.004	0.136±.003	2.20±.04
83 1 26	700	6.202±.003	0.130±.002	2.10±.04
6 26 52	800	6.289±.002	0.098±.002	1.59±.03
10 44 49	700	6.213±.003	0.100±.002	1.65±.03
6 42 52	800	6.335±.002	0.103±.002	1.54±.03
53 52 83	700	6.122±.003	0.129±.002	2.10±.04

TECHNIQUE AND MATERIAL

Turning our attention to the biometrical technique we shall give here only the final stage of its development. The most important sources describing the methods of measuring the tongue length are papers of Chochlov (22) and Loginov (37). The best method to ensure that the tongue shall be fully extended is to kill the bees (slightly anesthetized by means of the usual anesthetics adopted in entomological practice—ether, calcium cyanide and others) by dropping them into boiling water. This method was used in all investigations on the tongue length of Russian bees. Killed bees may be preserved in 70 per cent alcohol, or may be immediately macerated in a 5 per cent solution of KOH until the muscles are dissolved. Dissected tongues are measured usually in water or in 70 per cent alcohol. If they have to be preserved for a while a very convenient medium is glycerin jelly or simply glycerin. Practically the same results may be obtained by using the following method of preserving the material. Bees killed in a cyanide bottle are immediately placed on a layer of cotton and the tongues everted by means of thin forceps. This method was used in preserving material from Abchasia (Caucasus). All measurements in the United States have been made on bees sent alive in queen cages, killed in boiling water and dissected and mounted in glycerin. It was found that the tongues measured on material which was preserved in dry condition without any precautions give a length which is about 6.5 per cent smaller than the normal. Our material on Russian and Caucasian bees (other than those from Abchasia) was sent to us dry in packages and was not used therefore for extensive measurements of the tongue length. The material on Italian bees from Italy was killed in boiling water and preserved in 70 per cent alcohol up to the moment of maceration in 5 per cent solution of KOH (10–15 minutes of boiling) and dissection.

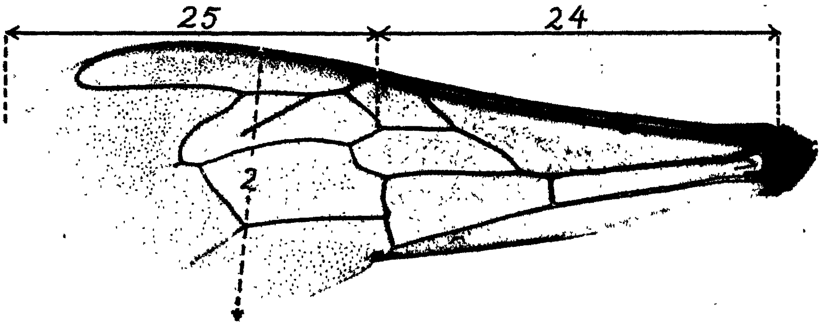

FIG. 2. MEASUREMENTS ON THE WING
The wing shows the intercubitus vein incompletely developed. (From Alpatov, 1928.)

In our study on Middle Russian and Ukranian bees twenty-five different characteristics were measured. In the subsequent work on other bee races, for the sake of saving time, eight of these measurements were omitted. Therefore in our present discussion we shall consider only those in the following list. In this list the numbering of the characters remains unchanged from that in our paper (9) mentioned above. This makes it easier to compare the old measurements with new ones.

(2) The width of the right wing (see Fig. 2).
(24) Proximal length of the wing (See Fig. 2).
(25) Distal length of the wing (See Fig. 2).
(3) Number of hooks on the hind wing.
(16) Length of the submentum measured along the median line (See Fig. 3).
(15) Length of the mentum (See Fig. 3).
(14) Distance from the distal end of the mentum to the narrowing on the ligula (See Fig. 3).
(13) From the narrowing to the end of ligula (See Fig. 3). (This double measuring of the ligula was used by the author during his work in Moscow, where a convenient magnification permitting the measurement of the whole length of the ligula at once was not available. During our work in the United States such a magnification was found and used.)
(8) Second sternum (See Fig. 4).
(22) Maximal length of the first wax sternum (See Fig. 5).
(21) "Length" of the first wax gland surface (See Fig. 5).
(10) Width of the first wax gland (See Fig. 5).
(11) Third tergum of the abdomen. (The first tergum of the abdomen represents a convex scale; the second, being under the cover slide, is apt to give as a rule numerous clefts; the third is therefore the most convenient one. This was also proposed by Armbruster (16). (See Fig. 7.))
(5) Length of the basal joints of the tarsus (See Fig. 6).
(4) Length of the tibia. (In case the upper end of the tibia cannot be seen distinctly enough, a slight pressing on the cover slide makes the joint easily determinable.)
(23) Length of the femur (See Fig. 6).
(26) Length of the yellow stripe along the front edge of the third tergum.

In our work on Middle Russian and Ukranian bees (9) we measured the yellow band on the second abdominal tergum, expressing the length of the band as per cent of the length of the whole tergum. In our investigation of other races, and particularly light colored ones, it was decided to measure the yellow band on the third tergum, the second one being sometimes completely deprived of the black stripe along the hind edge. It was decided to measure the length of the yellow band not on the median line of the tergum but a little to the right or

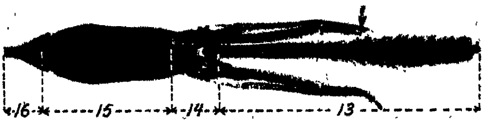

FIG. 3. MEASUREMENTS ON THE TONGUE

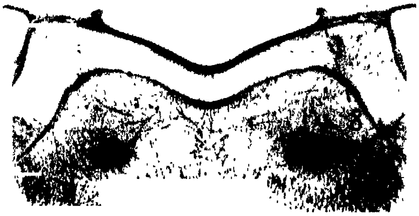

FIG. 4. MEASUREMENTS OF THE SECOND STERNUM

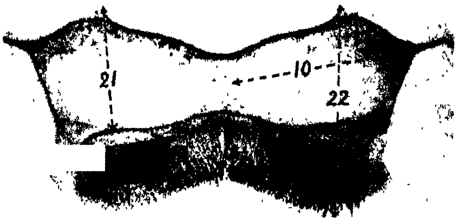

FIG. 5. MEASUREMENTS ON THE FIRST WAX STERNUM

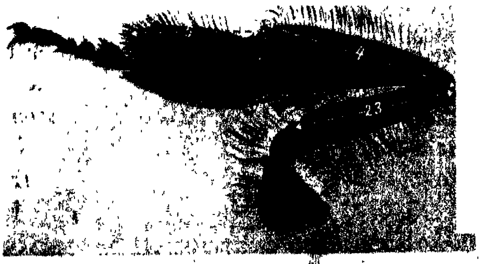

FIG. 6. MEASUREMENTS OF THE DIFFERENT JOINTS OF THE HIND LEGS

to the left of it. This was done because the black band is not so sharply defined in the middle as it is a little to the sides (See Fig. 7).

The wings were cut off before putting the insects into KOH. Even a short boiling (15–20 minutes) in KOH makes the wings useless for measurement. An ocular micrometer in an N.2 ocular was used during the whole investigation. Different objectives have been used, depending upon the size of the character to be measured and the length of the microscope tube. The most convenient systems were N.1 C and N.1 Reichert and N.2 Leitz. In measuring the wings in the drones a binocular was used. It must be noted that for comparative biometrical studies only very good object micrometers can be recommended. Two kinds of them must be distinguished. The first is prepared by a photographic method and is not very accurate, the other has a scale scratched by means of a dividing machine provided with a diamond.

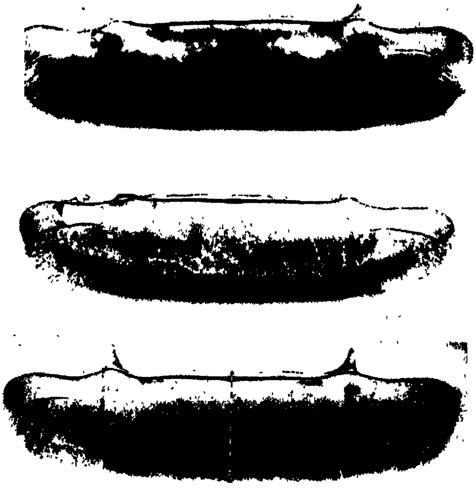

Fig. 7. Measurement of the Third Tergum of Abdomen

Third tergum of a Ukrainian bee (queen sent from Kursk) developed in Moscow, of an Italian worker bee born from an Italian queen shipped to Caucasus and of an Americanized Italian bee.

All frequency distributions have been made in divisions of the ocular micrometer, and only afterwards have the biometrical constants been converted into millimeters. It was found very convenient to calculate the ratio-indices using the formulas given by Pearson (64) and Pearl (63).

We calculated the biometrical constants for each of our 45 groups of bees included in Table 7 separately. Afterwards, in order to get more reliable constants with smaller probable errors it was decided to group the material according to the place of origin. The biometrical constants of these groups have been deduced from the constants of the 45 groups by using the following formulas:

$$M = \frac{M_1 n_1 + M_2 n_2 + M_3 n_3 \cdots\cdots}{N}$$

$$\sigma_m = \sqrt{\frac{n_1(\sigma^2_{m1} + d^2_1) + n_2(\sigma^2_{m2} + d^2_2) + n_3(\sigma^2_{m3} + d^2_3 \cdots}{N}}$$

where M is the arithmetical mean of the combined group; σ_m is the standard deviation of the combined group; n_1, n_2, n_3 . . . . represent the number of cases in separate groups; N is the whole number of cases; σ_{m_1}, σ_{m_2}, σ_{m_3} . . . . are the standard deviations in separate groups; d_1, d_2 are the deviations of separate M_1 . . . . from the general M. These formulas are given in a little different form by Yule (p. 142, 82).

Table 7 contains a list of the material worked out. The numbers from 1 to 33 correspond to the localities marked on the map (Fig. 8).

INFLUENCE OF EXTERNAL CONDITIONS UPON THE ORGANISM OF THE HONEY BEE

In this section we intend to bring together all the data available at the present moment on the influence of different external conditions upon the organism of the honey bee. It is due to a series of investigations of A. S. Michailov that this aspect of the variability of the honey bee is getting to be more and more clear. In his investigations he gives, as a rule, measurements of only five characters: (1) the tongue length, (2) the wing length, (3) wing width, (4) the sum of the length of the third and fourth tergum, and (5) the number of hooks on the hind wings. The measurements correspond in general to the scheme adopted in our own investigations. One difference is that we did not measure the length of the fourth tergum. Furthermore we did not add our measurements of the proximal and distal part of the wing length as is done in Michailov's articles. Only in one of his papers (52) does Michailov give the constants expressed in millimeters. In all others the constants are expressed in divisions of the ocular micrometer. We find it more convenient for purposes of comparison to give the final results in the metric system. In all the tables taken from Michailov's articles we recalculated the constants, expressing them in millimeters. Previous experience demonstrated the importance of the calculation of indices for characterizing constitutional types in bees. It seemed therefore just to calculate them for Michailov's experimental bees. As it was not possible to calculate from Michailov's data the coefficients of correlation indispensible for using the index formula (Michailov's article containing only frequency distribution) we substituted for the required coefficient of correlation the mean of those obtained in our work on Middle Russian and Ukrainian bees. These averaged coefficients of correlation are as follows: $r = .136$—correlation between the length of the tongue and the length of the third tergum; $r = .203$—the correlation of the wing length and the third tergum; and $r = .593$—the correlation of the length and width of the wings. The calculated proportions, by this method, are given in Table 3, *supra*, and other tables based upon Michailov's data.

The data on the influence of different conditions upon the organism of the honey bee available at the present moment may be classified in the following manner:

(1) The seasonal variation of the honey bee.
(2) The influence of the temperature during the development of the sealed brood.
(3) Size of the cells:
    (a) bees developed in worker cells and in drone cells.
    (b) bees developed in old and new cells.
(4) Nutrition:
    (a) length of larval feeding.
    (b) age of nurse bees.
(5) Influence of the age of the imago on the dimensions of the body.
(6) Strength of the colony.

The observations on seasonal variation of the honey bee have been done by Michailov. He calculated constants for bees emerging at five different times in the breeding season during the summer of the year 1926. The bees had their development in the same comb put in the middle of the strong colony. The queen of this colony was marked in the spring so that there is no doubt that all five successive groups of bees were genetically identical.

Newly emerged bees were collected directly from the comb. The accompanying Table 8 shows that the chitin of the worker undergoes distinct changes during the summer. Especially pronounced is the difference between bees emerging during the first part of the summer (before the swarming period) and bees which emerged after July 20. The right hand column shows that the increase in size toward the end of the summer is most pronounced in the wing length; then come the characters on the abdomen, and last is the tongue. The number of hook

TABLE 7

List of the material analysed

NUMBER	LOCALITY	RACE	NUMBER OF COLONIES	NUMBER OF INDIVIDUALS	CHARACTERS STUDIED	IN WHAT GROUP INCLUDED FOR CALCULATION OF CONSTANTS
1	Radomisl, Kiev district	*A. mellifera mellifera* L.	6	64	Wing characters	50° S. Russia
2	Valuiki, Voronezh district	*A. mellifera mellifera* L.	11	68	All characters	50° S. Russia
3	Volchansk, Voronezh district	*A. mellifera mellifera* L.	7	43	All characters	50° S. Russia
4	Rossosch, Voronezh district	*A. mellifera mellifera* L.	10	48	Wing characters	50° S. Russia
5	Kriusha, Voronezh district	*A. mellifera mellifera* L.	6	60	Wing characters	50° S. Russia
6	Rovenki, Voronezh district	*A. mellifera mellifera* L.	9	92	Wing characters	50° S. Russia
7	Rudnja, Saratov district	*A. mellifera mellifera* L.	5	50	Wing characters	50° S. Russia
8	Krasnojar, Smolensk district	*A. mellifera mellifera* L.	6	60	Wing characters	55° M. Russia
9	Basmanovo, Smolensk district	*A. mellifera mellifera* L.	7	100	Wing characters	55° M. Russia
10	Smolensk	*A. mellifera mellifera* L.	10	100	Wing characters	55° M. Russia
11	Bashkirovka, Kaluga district	*A. mellifera mellifera* L.	6	59	Wing characters	55° M. Russia
12	Lukianov, Kaluga district	*A. mellifera mellifera* L.	6	55	Wing characters	55° M. Russia
13	Bykscheevo and Romanovo, Kaluga district	*A. mellifera mellifera* L.	6	62	Wing characters	55° M. Russia
14	Malojaroslavetz, Kaluga district I	*A. mellifera mellifera* L.	6	61	Wing characters	55° M. Russia
15	Malojaroslavetz, Kaluga district II	*A. mellifera mellifera* L.	6	61	Wing characters	55° M. Russia
16	Novoje, Tula district	*A. mellifera mellifera* L.	6	60	Wing characters	55° M. Russia
17	Kashira, Moscow district	*A. mellifera mellifera* L.	10	58	All characters	55° M. Russia
18	Kolomna, Moscow district	*A. mellifera mellifera* L.	8	48	All characters	55° M. Russia
19	Zaraisk, Ryazan district	*A. mellifera mellifera* L.	4	40	Wing characters	55° M. Russia
20	Ryazan	*A. mellifera mellifera* L.	6	50	Wing characters	55° M. Russia
21	Ufa	*A. mellifera mellifera* L.	9	100	Wing characters	55° M. Russia
22	Uisk, Uralsk district	*A. mellifera mellifera* L.	6	52	Wing characters	55° M. Russia
22a	Chistopol, Kasan	*A. mellifera mellifera* L.	10	99	Wing characters	55° M. Russia
23	Stavropol, N. Caucasus	Intermediate form	?	156	Wing characters	N. Caucasus
24	Maikop, N. Caucasus	Intermediate form	many	100	All characters	N. Caucasus
25	Tiflis	*A. mellifera caucasica* Gorb.	10	50	All characters	Central Mountains
26	Svanetia	*A. mellifera caucasica* Gorb.	several	36	All characters	Central Mountains
27	Kutais	*A. mellifera caucasica* Gorb.	collected on flowers	32	All characters	Central Mountains

28a	Golovinka, Abchasia I	Intermediate forms	9	45	Wing Characters	Abchasia
28b	Schache, Abchasia II	Intermediate forms	12	60	Wing characters	Abchasia
28c	Kichmai, Abchasia III	Intermediate forms	10	41	All characters	Abchasia
29	Adler, Abchasia	Intermediate forms	about 10	66		Abchasia
30	Migri, Transcaucasus	*A. mellifera remipes* Gersch.	3	29	All characters	
31	Delidjan, Transcaucasus	*A. mellifera caucasica* Gorb.	4	40	All characters	
32	Pennsylvania	*A. mellifera ligustica* Spin.	10	50	Wing characters	Italian bees. U. S. A.
33	Kentucky	*A. mellifera ligustica* Spin.	10	50	Wing characters	Italian bees. U. S. A.
34	Alabama, I apiary	*A. mellifera ligustica* Spin.	10	50	Wing characters; ½ of the specimens were measured for all characters	Italian bees. U. S. A.
35	Alabama, II apiary	*A. mellifera ligustica* Spin.	10	50	Wing characters; ½ of the specimens were measured for all characters	Italian bees. U. S. A.
36	Ohio, I apiary	*A. mellifera ligustica* Spin.	10	50	Wing characters; ½ of the specimens were measured for all characters	Italian bees. U. S. A.
37	Ohio, II apiary	*A. mellifera ligustica* Spin.	10	50	Wing characters; ½ of the specimens were measured for all characters	Italian bees. U. S. A.
38	New York, Cornell University apiary	*A. mellifera ligustica* Spin.	10	50	Wing characters	Italian bees. U. S. A.
39	New York	*A. mellifera ligustica* Spin.	10	50	Wing characters	Italian bees. U. S. A.
40	Italy, Bologna	*A. mellifera ligustica* Spin.	10	50	All characters	
41	Caucasus (queens imported from Italy)	*A. mellifera ligustica* Spin.	7	50	Wings and tongues	
42	Ontario	*A. mellifera mellifera* L.	10	50	Wings and tongues	Black bees. U. S. A.
43	North Carolina	*A. mellifera mellifera* L.	10	50	Wings and tongues	Black bees. U. S. A.
44	Florida	*A. mellifera mellifera* L.	10	50	Wings and tongues	Black bees. U. S. A.
45	Colorado	*A. mellifera caucasica* Gorb.	10	50	All characters	

TABLE 8

Seasonal variation of the honey bee

(From Michailov, 1927)

		JUNE 5	JUNE 29/30	JULY 20/21	AUGUST 17/18	SEPTEMBER 6/11	DIFFERENCE I-V
		I	II	III	IV	V	
Tongue length	M	6.125±.008	6.189±.006	6.280±.006	6.238±.006	6.282±.006	.157±.010 R = 15.7
	C*	2.04±.10	1.54 ±.07	1.49 ±.07	1.48 ±.07	1.47 ±.07	
	N	99	99	100	96	99	
Length of the wing	M	9.175±.012	9.258±.010	9.525±.010	9.458±.008	9.590±.009	.415±.015 R = 27.7
	C	1.88 ±.09	1.54 ±.07	1.49 ±.07	1.23 ±.06	1.47± .07	
	N	100	100	100	100	100	
Width of the wing	M	3.063±.005	3.095±.004	3.186±.004	3.185±.004	3.200±.006	.137±.008 R = 17.1
	C	2.45 ±.11	2.11 ±.10	2.00 ±.10	1.95 ±.09	2.60 ±.12	
	N	100	100	100	100	100	
Hooks	M	22.06±.10	22.00±.10	22.02±.11	21.90±.12	22.07±.10	.01±.14 R = 0.0
	C	6.87±.33	6.95±.33	7.12±.34	8.43±.40	6.84±.33	
	N	100	100	100	100	100	
Tergum (III + IV)	M	4.752±.008	4.808±.007	4.954±.007	4.916±.006	4.937±.006	.185±.010 R = 18.5
	C	2.58 ±.12	2.06 ±.10	2.19 ±.10	1.80 ±.09	1.76 ±.08	
	N	100	100	100	100	100	
Tongue length: tergum (III + IV)	M	128.97±.27	128.77±.21	126.82±.21	126.93±.19	127.28±.18	1.69±.32 R = 5.3
	C	3.06±.15	2.40±.12	2.48±.12	2.17±.10	2.13±.10	
Wing length: tergum (III + IV)	M	193.19±.37	192.62±.30	192.35±.31	192.45±.25	194.30±.27	1.11±.46 R = 2.4
	C	2.87±.14	2.31±.11	2.39±.11	1.96±.09	2.05±.10	
Breadth of wing: length of wing	M	33.39±.05	33.43±.04	33.45±.05	33.68±.04	33.37±.05	.02±.07 R = 0.3
	C	2.02±.10	1.72±.08	2.11±.10	1.58±.08	2.10±.10	

remains constant throughout the whole period covered by the observation. Turning our attention to the changes in proportions of the body we find that it is only the tongue index which shows a definite increase in the bees in late summer. We agree entirely with Michailov in the statement that in racial investigations special attention must be paid to obtaining material belonging to the same biological moment. The best time seems to be in the fall and winter. In all our original measurements the material was sent to us in the latter part of the summer or immediately after wintering.

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* In all tables C signifies the coefficient of variation.

Concerning the explanation of the seasonal variation we are not able at the present moment to express a definite opinion. As will be shown later on the organism of the bee can be influenced by a whole set of environmental factors. Very likely all of these change considerably during the season. At the present moment we know next to nothing about the seasonal changes of any of these factors. We are inclined to think that the feeding is one of the most important factors. It has been known for years that during the honey flow the bees get "fat". On the other hand in beekeeping literature are scattered numerous observations on the production of dwarf bees. Especially pronounced is this phenomenon among Italian bees, which react to the disappearance of the nectar secretion even by completely discontinuing brood feeding and throwing them out of the hive.

TABLE 9

Influence of the temperature of development of the sealed brood on the adult worker bees. Colony 63

(After Michailov, 1927)

		TEMPERATURE 35°	DIFFERENCE AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	TEMPERATURE 30°
Tongue	M	5.824±.008	.230±.013	5.594±.010
	C	2.02 ±.10	R = 17.8	2.41 ±.12
	N	99		88
Length of the wing	M	8.917±.011	.284±.024	8.633±.021
	C	1.88 ±.09	R = 11.8	3.40 ±.17
	N	100		87
Width of the wing	M	3.009±.005	.009±.008	3.000±.006
	C	2.31 ±.11	R = 1.0	2.93 ±.15
	N	100		87
Number of hooks	M	20.76±.12	.15±.16	20.91±.11
	C	—	R = 0.9	—
Tergum (III + IV)	M	4.580±.007	.214±.010	4.794±.007
	C	2.39 ±.11	R = 21.4	2.17 ±.11
	N	100		90
Tongue: tergum (III + IV)	M	127.23±.25	10.50±.35	116.73±.25
	C	2.91±.14	R = 30.0	3.01±.15
Length of wing: tergum (III + IV)	M	194.79±.36	14.65±.59	180.14±.47
	C	2.72±.13	R = 24.8	3.64±.19
Width of wing: tergum (III + IV)	M	33.75±.04	1.02±.08	34.77±.07
	C	1.92±.09	R = 12.75	2.88±.15

The influence of the temperature of the surroundings on the sealed brood and nymphae was also shown by Michailov (46). The first experiment consisted in putting sealed brood into two incubators

TABLE 10

Influence of the development in drone and worker cells

(Michailov, 1927)

		WORKER BEES FROM DRONE CELLS	DIFFERENCES	WORKER BEES FROM WORKER CELLS
Tongue	M	6.367±.016	.293±.021 R = 14.0	6.074±.013
	C	2.98 ±.18		3.47 ±.16
	N	65		112
Length of the wing	M	9.574±.027	.250±.033 R = 7.6	9.324±.019
	C	2.97 ±.18		2.14 ±.14
	N	63		50
Width of the wing	M	3.238±.010	.066±.013 R = 5.1	3.172±.009
	C	3.25 ±.20		2.97 ±.20
	N	63		50
Hooks	M	20.25±.18	.35±.25 R = 1.4	20.60±.18
	C	9.26 ±.56		9.26 ±.62
	N	63		50
Tergum (III + IV)	M	5.047±.020	.211±.022 R = 9.6	4.836±.009
	C	4.27 ±.26		1.87 ±.13
	N	63		50
Weight in grams	M	0.1451±.010	.148±.013 R = 11.4	0.1303±.008
	C	10.23 ±.47		9.95 ±.44
	N	106		114
Tongue: tergum (III + IV)	M	126.36±.52	.73±.60 R = 1.2	125.63±.35
	C	4.89±.29		3.71±.20
Length of wing: tergum (III + IV)	M	189.99±.75	2.86±.88 R = 3.25	192.85±.46
	C	4.67±.28		2.49±.17
Width of wings: length of wings	M	33.83±.08	.19±.11 R = 1.7	34.02±.08
	C	2.82±.17		2.42±.16

running at 30° and 35°C. It did not give bees differing in any respect. In the opinion of the author this is due to the inexact regulation of the incubators, and to the fact that the sealed brood was taken into the laboratory in a comparatively advanced stage of development (in the 35° incubator the bees emerged after seven and one half days, in the 30° incubator after ten days). In the second experiment the brood put in different temperatures was apparently just sealed. The emergence in the temperature of 35°C. began after fourteen days, and in the temperature of 30°C. three days later. Special pains were taken to expose to different conditions of temperature brood genetically identical (taken from the same part of the frame from one hive). Dishes with water put in the incubators kept the air moist.

No statistically significant differences were obtained in the first experiment; we reproduce therefore in Table 9 only the results of the second experiment. The following conclusions were drawn by Michailov: (1) the "cold" bees have a shorter tongue and wing length than the "warm" ones; (2) the "cold" bees are larger in respect to the length of terga. We add two other conclusions based on our calculations of indices: (3) the "cold" bees have *relatively* short tongues and wings; (4) the "cold" bees have *relatively* broad wings. These ambiguous results—the decrease of some characters in size and the increase in the size of the abdomen of the bees kept at low temperature, can very likely be explained by the following assumption. The period of a sealed brood consists biologically of several different stages; larva, subpupa, and pupa. It is very likely that the development of the characters studied takes place during different stages of the whole development in a sealed cell. Therefore the same factor, the temperature (and very probably the changed humidity) may influence different characters in a quite different way. It would be very important to repeat the experiment, using different temperatures during the different stages of the whole development in sealed cells.

The fact that queens sometimes lay fertilized eggs in drone cells, which lead to a development of worker bees in unusually large cells, has been reported several times in the beekeeping literature. Years ago a Russian scientist Martynov (38) attempted to show that the worker bees developed in drone cells have a longer tongue than those developed in worker cells. Michailov (52) took occasion to study this comparatively rare abnormality in the egg laying activity of the honey bee. Table 10 represents his results. In the original form the constants were provided with mean errors. We calculated probable errors which are used throughout our whole investigation.

We see that in all measurements the bees developed in larger cells exceed the controls developed in regular worker cells. The proportions of the body remain unchanged.

Very close to the experiment just described is another experiment consisting in putting in one hive combs of different age (Michailov, 46). It is a popular opinion among beekeepers that in colonies where the combs are old and have been used for brood rearing for many generations the emerging bees are small. Two separate experiments were carried out. The one where the difference between the size of the two groups of cells was not very pronounced did not give definite differences in body measurements. On the other hand the experiment in which the colony N 112 was taken gave very clear results. After the experiment was over the combs were filled with paraffin and longitudinal and cross sections were prepared with a microtome. The measurements of the sections give the material for judging the dimensions of the cells and the number of generations which had their development in the cells before the experiment. Table 12 shows these data. It can be seen that the number of cocoons for the dark comb is 16.1. That means that at least 15 generations have lived there before the generation which was taken for measurement. Another peculiarity of old combs is a deeper and narrower cell. Table 11 shows the differences in physical characteristics of bees developed in old and new combs. All characters show a smaller size in bees developed in the narrower cells. Even the number of hooks, which is usually very constant under the influence of different environmental factors, here shows a pronounced decrease. As for the proportions, the smaller, dark comb bees have a relatively longer tongue than the white

TABLE 11

Influence of age of the comb (white and dark combs) on worker bees

(From Michailov, 1927)

		WHITE COMB	DIFFERENCE AND R = DIFF./P.E.	DARK COMB
Tongue	M	6.275±.012	.065±.016 R = 4.1	6.210±.010
	C	2.50 ±.13		1.63 ±.08
	N	79		100
Length of the wing	M	9.425±.016	.193±.017 R = 11.4	9.232±.010
	C	2.47 ±.12		1.67 ±.08
	N	96		99
Width of the wing	M	3.151±.005	.057±.006 R = 9.5	3.094±.004
	C	2.35 ±.11		1.88 ±.09
	N	96		99
Hooks	M	21.79±.12	.84±.16 R = 5.25	20.95±.10
	C	7.96±.39		6.96±.33
	N	97		99
Tergum (III + IV)	M	4.830±.010	.139±.012 R = 11.6	4.691±.006
	C	2.95 ±.14		2.03 ±.10
	N	97		100
Tongue: tergum (III + IV)	M	130.02±.34	2.40±.40 R = 6.0	132.42±.22
	C	3.60±.18		2.42±.12
Length of wing: tergum (III + IV)	M	195.28±.46	1.59±.55 R = 2.9	196.87±.31
	C	3.44±.17		2.35±.11
Width of wing: length of wing	M	33.44±.05	.08±.06 R = 1.3	33.52±.04
	C	2.18±.11		1.61±.08

comb ones. Both experiments with drone cells and the dark combs show the influence of larger cells in increasing the dimensions of the bee's body.

Turning our attention to nutrition, we must emphasize that in the development of the honey bee nutrition plays an extremely important rôle. Besides that, we must remember that it is a change in nutrition which produces intermediate forms between the worker bee and the queen, as was discovered by Pastor Klein (see 18 and 34), Koshevnikov (34) and Götze (27), and Becker (18). Our paper (14) is also devoted to the discussion of this problem.

TABLE 12

Differences between the white and dark combs used in the colony N. 112

(From Michailov, 1927)

	AVERAGE NUMBER OF COCOONS	AVERAGE DIAMETER OF THE CIRCLE INSCRIBED IN THE CROSS SECTION OF THE CELL (IN MM.)	AVERAGE DEPTH OF THE CELL (IN MM.)
White comb........	1	5.129	11.365
Dark comb.........	16.12	4.827	11.841

During the author's residence at Cornell University (1927) an attempt was made to study the influence of under-nourishment of larvae upon the characteristics of adult bees. The experiment consisted in putting the unsealed brood in an incubator running at 34.5°C. The brood was taken from a comb approximately one day before normal sealing. On the following day when the cells situated in the neighborhood of the place from which a piece of comb had been taken the day before had been sealed by the bees, they were also put in the incubator, serving as control. The pieces of comb with unsealed larvae put in the incubator were covered with pieces of artificial comb foundation as a substitute for the natural capping by working bees. The larvae wove cocoons as usual and the emerging bees were collected according to the above described rules and preserved in alcohol. The bees emerging from the brood which was not sealed normally apparently did not get food enough, as compared with brood sealed by worker bees at the normal time. Table 13 shows that the absolute dimensions of characters measured on experimental underfed bees are smaller than in the controls. Even the number of hooks is reduced under the influence of underfeeding. The indices were calculated according to the scheme used in all our racial investigations (see below) and do not show any changes in proportions of the body of the experimental insects as compared with controls. This experiment has already been mentioned in our paper on the variation of the hooks (11) in connection with the occurrence in experimental bees of a very high percentage of individuals with an incomplete development of the second intercubitus vein.

Recent investigations of Rösch (70) have shown that among the workers of a bee colony there exists a very definite division of labor. In the feeding of the brood, bees 6–13 days old are engaged. A biometrical test of this conclusion has been made by Michailov in the following experiment. A rather strong colony, No. 121, was moved, in the middle of a good sunny day, from its usual place, on which was set an empty hive provided with frames with pollen and honey. The queen of the colony was transferred to the new hive and kept in a cage until the sealing of the experimental brood took place. All the bees of the colony N 121 which had been in the field or had left the old colony after the transfer, came back to the place where the colony used to stay

TABLE 13

Worker bees developed from underfed larvae compared with controls

CHARACTERS	CONTROL			DIFFERENCES AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	EXPERIMENTAL (UNDERFED)		
	Mean	Coefficient of variation	N		N	Mean	Coefficient of variation
8	2.307±.005	1.95±.14	44	.088±.014 6.3	28	2.219±.013	4.56±.41
10	2.337±.005	2.06±.15	43	.100±.016 6.25	25	2.237±.015	5.01±.48
21	1.554±.005	2.96±.21	44	.061±.011 5.5	25	1.493±.010	5.18±.49
22	2.757±.006	2.02±.15	44	.102±.016 6.4	25	2.655±.015	4.26±.41
Tongue length	6.034±.013	2.24±.16	43	.130±.024 5.4	31	5.904±.020	2.73±.23
5	2.033±.005	2.63±.19	45	.091±.011 8.2	31	1.942±.010	4.41±.38
4	3.169±.006	2.03±.14	45	.122±.015 8.1	31	3.047±.014	3.88±.33
23	2.609±.005	1.74±.12	45	.103±.011 9.4	31	2.506±.010	3.33±.29
Hooks	20.60±.15	7.33±.52	45	0.89±.17 5.24		19.71±.09	7.39±.33
25	4.353±.012	2.65±.19	45	.161±.026 6.2	31	4.192±.023	4.43±.38
24	4.696±.010	2.10±.15	45	.171±.023 7.4	31	4.525±.021	3.77±.32
2	3.115±.007	2.33±.17	45	.095±.012 7.9	31	3.020±.010	2.67±.23
26	1.852±.034	18.23 —	45	.058±.051 1.1	31	1.794±.038	17.48 —
11	2.241±.004	1.87±.13	45	.086±.010 8.6	31	2.155±.009	3.61±.31
21:22	56.36 ±.12	2.02±.15	44	.14 ±.18 0.77	25	56.22±.18	2.32±.22
5:11	90.75±.32	3.47±.25	45	.63 ±.42 1.5	31	90.12±.28	2.58±.22

TABLE 13—*Concluded*

CHARACTERS	CONTROL			DIFFERENCES AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	EXPERIMENTAL (UNDERFED)		
	Mean	Coefficient of variation	N		N	Mean	Coefficient of variation
4:11	141.45 ±.35	2.43±.17	45	.04 ±.52 0.0	31	141.41 ±.39	2.26±.19
23:11	116.46 ±.28	2.35±.17	45	.13 ±.43 0.1	31	116.33 ±.33	2.32±.20
25:24	92.70 ±.16	1.74±.12	45	.06 ±.31 0.0	31	92.64 ±.27	2.37±.20
2:24	66.39±.11	1.67±.12	45	.40 ±.23 1.7	31	66.79±.20	2.53±.22
26:11	82.65±1.52	18.33 —	45	.65±2.33 .28	31	83.30±1.76	17.42 —

before the transfer and populated the new hive. As a result of this procedure the old hive transferred to a new place was deprived of field bees, which are as a rule older than eleven days, and contained only hive bees—in other words, young bees. The opposite was the case in the new hive where only field bees were present. A piece of comb with eggs and new born larvae was taken from another colony (No. 39) and was divided into two pieces. They were then put into two hives populated by bees of different ages. The results of a biometrical investigation are shown in Table 14. The bees brought up by old nurses have larger wings and tergums than those fed by young bees. The proportions of the body show that the smaller bees fed by young nurses have comparatively long tongues. Michailov's conclusion is that the experiment does not bring any evidence in support of Rösch's conclusions. We do not believe that it is wise to attribute the differences observed to the age of the nurse bees only. The conditions in both hives were different in many respects, which is also admitted by Michailov. The absence of the queen in one of the hives (with young bees) might be responsible for many peculiarities in the behavior of the members of the colony.

We will not put much stress on Michailov's conclusions concerning the changes of bees with age (49). The experiment consisted in measuring new born bees and bees previously marked with color marks at the age of 25 days. The observed differences—reduction in the length of the tongue and in the number of hooks and increase in the wing width—might be caused not by aging but by selection, the marked bees being placed in a hive from which they could fly out and get lost.

Some very interesting statistical conclusions concerning the relationship between the strength of the colony and its average tongue length can be drawn from the material published by V. P. Michailov, Director of the Experimental Apiary of the Perm State University. He measured (57) the tongue length in 23 colonies of bees, taking about 200 individuals from each hive. The colonies were classified as strong, middling, and weak ones. This classification has not, of course, the precision of a quantitative evaluation but nevertheless it expresses the general impressions as to the quantity of bees in the hive, the degree of working activity, etc. Calculating the coefficient of correlation between the strength and the average tongue length we obtain $r = .489 \pm .107$. We may thus conclude with tolerable certainty that the stronger colonies have longer tongues. In a recent paper (48) A. S. Michailov found that there is no correlation between the strength of the colony (number of bees in the colony) and the size of the different parts of the exoskeleton. A positive correlation was found between the strength of the colony and the average weight of bees caught at the entrance of the hive when they were ready to leave the hive, flying in the field. The coefficient of correlation was found to be .591 ± .080. Michailov's calculations were based on measurements of

TABLE 14

Biometrical constants of worker bees reared by old and young nurse bees. Each group is represented by 100 specimens
(From Michailov, 1928)

		REARED BY OLD NURSE BEES	DIFFERENCE AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	REARED BY YOUNG NURSE BEES
Tongue	M	6.205±.008	.010±.011 R = 0.9	6.195±.007
	C	1.84 ±.09		1.69 ±.08
Length of the wing	M	9.307±.009	.076±.011 R = 6.9	9.231±.007
	C	1.41 ±.07		1.20 ±.06
Width of the wing	M	3.187±.004	.051±.006 R = 8.5	3.136±.004
	C	1.95 ±.09		1.81 ±.09
Hooks	M	20.36 ±.10	.52 ±.14 R = 3.7	20.88±.10
Tergum (III + IV)	M	4.814±.006	.056±.008 R = 7.0	4.758±.006
	C	1.94 ±.09		1.86 ±.09
Tongue: tergum (III + IV)	M	128.94 ±.22	1.30±.29 R = 4.5	130.24 ±.19
	C.	2.48 ±.12		2.15 ±.10
Length of wing: tergum (III + IV)	M	193.39 ±.28	.68 ±.38 R = 1.8	194.07 ±.26
	C	2.15 ±.10		2.00 ±.10
Width of wing: length of wing	M	34.24 ±.37	.27 ±.50 R = 0.5	33.97±.33
	C	1.59 ±.08		1.46 ±.07

bees from thirty colonies of the Tula Apicultural Experimental Station. This lack of agreement with our conclusions based on data collected in Perm may perhaps find its explanation in the hypothesis that the Tula colonies were more uniform in respect to their strength than those from Perm. Anyhow the question should be investigated further.

Summing up the results discussed in regard to the change of proportions of the body we can draw only one conclusion. In the cases where all characteristics of the bees affected by experimental conditions showed a decrease (influence of the age of nurse bees, small cells, season of the year), smaller bees have relatively long tongues. In the case of the influence of temperature bees with shorter wings had relatively broader wings. These conclusions may help us to explain in the future some of the racial differences in the proportion of the body of the honey bee.

GEOGRAPHICAL VARIATION OF BEES FROM THE PLAIN OF EUROPEAN RUSSIA, ITALY AND NORTH CAUCASUS

Turning our attention to the geographical variation of the honey bee we must start with races of eastern Europe because the pioneer work on geographical variation was done there. This is not owing to chance. It is easy to observe laws in the geographical changes of characters in animals when the climate and other environmental factors change regularly and gradually. Such is just the case with the plain of European Russia, while it is not so in Western Europe, which is cut up by mountain chains. It is also not without importance that the Russian plain has always been politically one country, which has a certain advantage in studying conditions from the same point of view. In that respect conditions there resemble greatly those of North America. We are inclined to think that the American scientists, having long ago been interested in the geographical variation of animals, (remember the classical work of Allen on the geographical variation of birds) would not have neglected to make investigations of the geographical variation of the honey bee, had it not been for one circumstance.

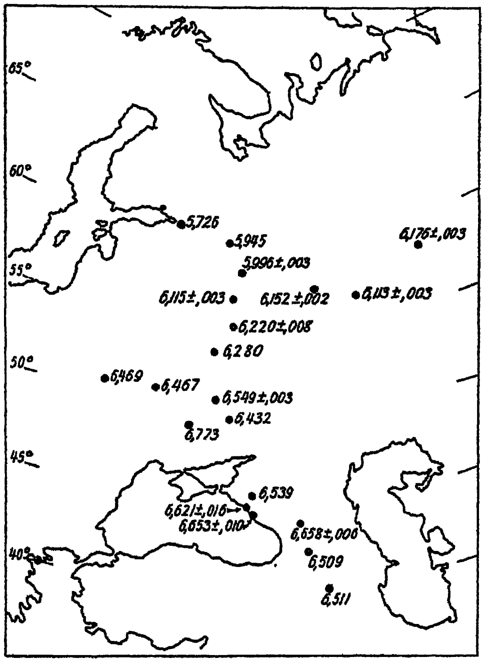

Fig. 8. Map of European Russia and Caucasus, Showing the Average Tongue Length of Bees from Different Localities

The averages are accompanied by probable errors only in cases when the examined bees have been collected from not less than five colonies.

The whole bee population of the New World is the result of a transportation of different bee races from Europe, the honey bee not being among the animals native to America.

As was stated above the tongue was the first organ to be studied from the point of view of variability which gave evidence of the existence of geographical variation (Michailov, 39). The map in figure 8 shows the results of tongue measurements

TABLE 15

Biometric constants of the tongue length in different localities in European Russia. In the table are included only data representing measurements based on a considerable number of colonies

LATITUDE	LOCALITY	MEAN IN MM.	STANDARD DEVIATION	COEFFICIENT OF VARIATION	NUMBER OF SPECIMENS	NUMBER OF COLONIES	SOURCE
58°	Perm	6.176±.002	.1133	1.83±.02	2000	20	W. P. Michailov, 1926. Alpatov, 1927.
$57\frac{2}{3}^{\circ}$	Jaroslawl	5.996±.003	.1421	2.37±.04	931	10	Alpatov, 1927
$56\frac{1}{3}^{\circ}$	Nizhni Nowgorod	6.152±.002	.1456	2.37±.03	1676	17	Kurotschkin, 1928
$55\frac{3}{4}^{\circ}$	Moscow	6.115±.003	.1299	2.13±.03	1000	10	Alpatov, 1927
$55\frac{3}{4}^{\circ}$	Kasan	6.113±.003	.1544	2.53±.04	1000	20	Loginov and Alpatov, 1926
$54\frac{1}{5}^{\circ}$	Tula	6.220±.002	.1270	2.04±.02	2500	10	Alpatov and Tjunin, 1925
50°	Kharkov	6.549±.003	.1280	1.95±.03	800	8	Alpatov, 1927

TABLE 16

Biometrical constants for bees of Middle and South Russia, North Caucasus and Italy

CHARACTERS	CHARACTER NUMBER	1	2	3	4	R = $\frac{\text{DIFF.}}{\text{P.E.}}$ FOR THE DIFFERENCES BETWEEN THE MIDDLE RUSSIAN AND BEES FROM SOUTH RUSSIA, NORTH CAUCASUS AND ITALY		
		55° MIDDLE RUSSIA	50° SOUTH RUSSIA	NORTH CAUCASUS	ITALY	1–2	1–3	1–4
Length of the second sternum	8	2.453±.004	2.387±.005	2.391±.004	2.306±.005	10.0	10.3	24.5
Length of the first wax sternum	22	2.988±.007	2.858±.007	2.830±.005	2.732±.006	13.0	17.6	28.4
Length of the first wax gland surface	21	1.778±.005	1.632±.006	1.589±.004	1.511±.005	18.3	31.5	38.1
Width of the first wax gland	10	2.541±.006	2.423±.008	2.390±.005	2.302±.006	11.8	18.9	29.9
Length of the first tarsal joint	5	2.125±.004	2.095±.004	2.116±.005	2.081±.005	5.0	1.5	7.3
Length of the tibia	4	3.363±.006	3.293±.005	3.438±.005	3.225±.005	8.75	9.4	17.3
Length of the femur	23	2.738±.004	2.678±.004	2.777±.004	2.653±.005	10.0	6.5	14.2
Distal length of the wing	25	4.553±.002	4.499±.003	4.398±.003	4.333±.012	13.5	38.75	18.3
Proximal length of the wing	24	4.913±.002	4.871±.003	4.792±.004	4.713±.009	10.2	30.25	22.2
Width of the wing	2	3.166±.002	3.189±.003	3.071±.004	3.168±.008	7.7	23.8	0.2
Number of hooks	3	20.70 ±.04	21.08 ±.06	20.61±.06	21.51 ±.08	8.85	1.29	9.0
Length of the third tergum	11	2.345±.005	2.266±.006	2.257±.004	2.172±.005	9.9	14.7	19.2
Indices:								
21:22		59.53±.12	57.10±.13	56.15±.11	55.31±.15	13.5	19.9	22.2
5:11		90.69±.24	92.55±.26	93.79±.21	95.89±.33	5.3	9.69	12.7
4:11		143.48±.36	115.44±.41	152.40±.24	148.61±.45	3.6	20.7	8.8
23:11		116.81±.23	118.30±.32	123.00±.21	122.25±.38	3.7	20.0	12.4
25:24		92.68±.05	92.39±.08	91.67±.10	91.96±.25	3.2	9.1	2.9
2:24		64.46±.03	55.47±.05	64.50±.07	67.22±.14	16.8	0.6	23.0

on the plain of European Russia and Caucasus up to the present time. In order not to put much stress on data obtained from measurements of bees belonging to less than five colonies of a given locality the averages in this case are not provided with probable errors. It is perfectly clear that bees even of neighboring localities differ in the average length of tongue. At the same time we observe as a general rule that farther to the south the tongue is longer.

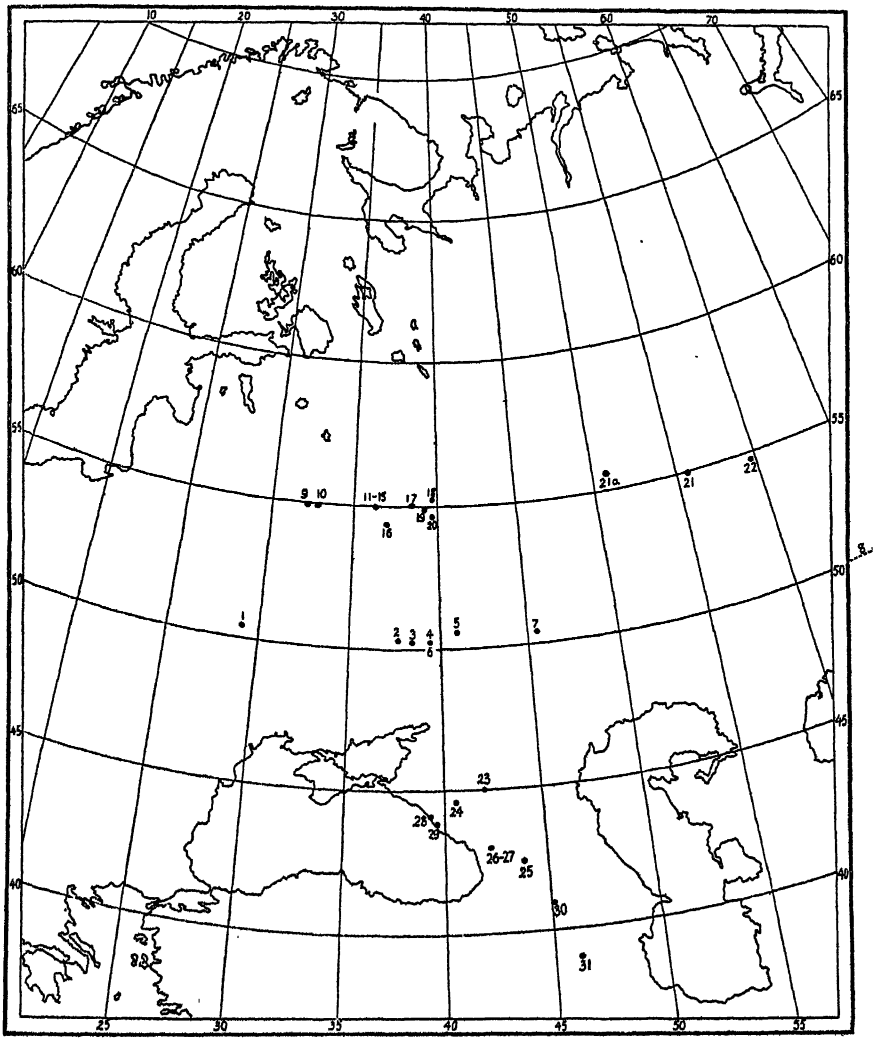

FIG. 9. MAP OF EUROPEAN RUSSIA AND CAUCASUS
The figures indicate localities where the material has been collected.

In one of our previous papers (5) (independently of Michailov, 42) we attempted to express in the form of a linear equation the relationship between the length of the tongue and the latitude of the locality. In recalculating this equation we used only the most reliable averages of the Kharkov, Tula and Moscow bees.

This equation is as follows: $y = 10.3219 - 0.07559\, x$, x standing for the latitude of the locality and y for the length of the tongue. Table 15 gives the best and most reliable data on the variation of the tongue length in European Russia. The variation of the tongue length of the Caucasian bees will be discussed later.

When the general trend in the variation of the tongue was sufficiently clear the question arose as to the variability of the other organs of the bee. Table 16 gives us the data on the variability of different organs of four groups of bees—Middle Russian, South Russian, North Caucasian, and Italian reared in Italy. For a moment we may leave the tongue and turn our whole attention to the variation of other organs. Let us for a while omit from the discussion the North Caucasians. The first conclusion is that the southern bees are smaller than the northern ones in absolute dimensions of the body. Only the number of hooks shows a pronounced increase toward the south. The data on wing characteristics are based on very large material from different parts of European Russia. The accompanying map of figure 9 shows the localities where the material was collected. (For hook variation see our special paper, 11.) The frequency curves of the variation of the number of the hooks of bees collected at 50° and 55° latitude are shown in figure 10. Another interesting exception to the rule of the decrease of the body dimensions toward the south is the fact that the width of the wings is even larger in South Russian than in Middle Russian bees.

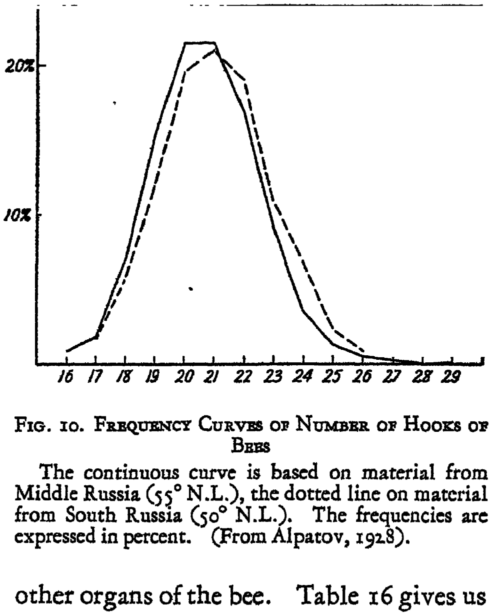

Fig. 10. Frequency Curves of Number of Hooks of Bees

The continuous curve is based on material from Middle Russia (55° N.L.), the dotted line on material from South Russia (50° N.L.). The frequencies are expressed in percent. (From Alpatov, 1928).

Turning our attention to the change in the body proportions we find many interesting regularities. The index of the wax gland shows a gradual decrease in the south, showing that the bees there have a less extensively developed wax producing surface of the third sternum. The indices of all the three joints of the hind legs show that the southern bees are comparatively long legged. It is also evident that in the south the bees have broader wings than in the north. The index expressing the distal length of the wing in percent of the proximal one shows that in the southern bees the distal part of the wing plays a smaller rôle in the wing length than in the case of the northern bees. The ratios of differences to their probable errors are, however, not very high.

The North Caucasian bees as compared with those from Middle Russia give nearly the same picture as the Italian ones. We shall mention only the discrepancies found. The absolute length of the leg joint is even larger than in Middle Russians. That gives as a result an extremely high value for leg indices. We shall later on find the same characteristic picture for all Caucasian races. The North Caucasian bees do not show any increase in the relative width of the wing. We do not know at the present moment any adequate explanation for this fact.

A preliminary report on the decrease in body size of the honey bee in southern localities was sent by us to be announced at the All German Beekeeper's Meeting on August 3–4, 1926 (see Götze, 27). Independently Michailov (40), in comparing measurements of the North Caucasian (Kuban) bees with those from Tula found that the Kuban (North Caucasus) bees are smaller than the Middle Russian (Tula) ones. Unfortunately his observations were based on measurements of bees belonging to only three colonies from the Kuban region and Tula.

Summing up the results obtained we can say that the southern constitutional type of the honey bee differs from the northern one by its smaller absolute size of body and extremities (the Caucasian bees being an exception in respect of the length of the extremities); its larger mouth parts; more developed wings (relatively); and smaller wax producing surface of the ventral segments. In order to make the statistically observed differences in the constitution of the body more instructive we prepared the schemes shown in figure 11. We want to point out that the scheme of north-south changes in the bee body constitution holds true only for localities situated in approximately the same degree of longitude.

Without any question the rules which have been observed on worker bees should be tested on other members of the bee colony. But the collection of adequate material on drones, and particularly on queens, is not a very simple matter. We attempted to compare two groups of drones from Middle and South Russia (Table 17). The southern drones are in all characters absolutely smaller than the northern ones (the differences in characters 24, 2, mentum+ligula and the number of hooks are not statistically very significant). Very interesting is the index 25:24 which is in accord with the trend observed on worker bees. The indices of the extremities show even a rather opposite trend to that found in the worker bees. We do not want to put much stress on the proportions of the drone's body, leaving this question for further investigations.

VARIATION OF THE BEE RACES CULTIVATED IN THE UNITED STATES

The bees cultivated in the United States have been introduced from Europe. The first bees brought over belonged to the black European races and originated apparently from England and Holland. Since the sixties of the last century a movement has arisen among American beekeepers toward the culture of yellow bees. Since that time, step by step, the black bees have been more and more replaced by yellow Italian bees, and partly by other light colored European races like the Cyprian. At the present time it is a difficult task to find places where the black bees are cultivated. It must further be said that the demand for yellow bees produced a strong selection of

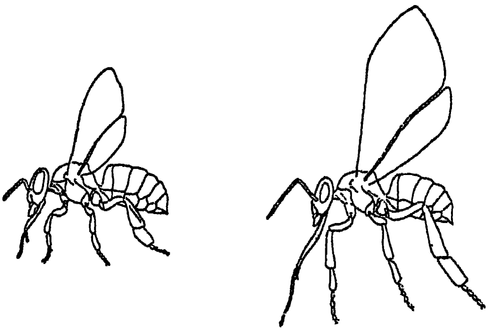
Northern Type Southern Type

FIG. 11. SCHEMATIC REPRESENTATION OF THE NORTHERN AND SOUTHERN CONSTITUTIONAL TYPES OF BEES
(From Alpatov, 1927)

TABLE 17

Biometrical constants of drones from Middle Russia and Ukraine

CHARACTER NUMBER	KALUGA (MIDDLE RUSSIA)		N	DIFFERENCE AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	N	N. WODOLAGA (SOUTH RUSSIA) UKRAINE	
	Mean	Coefficient of variation				Mean	Coefficient of variation
8	2.578±.006	2.47±.17	49	.112±.010 R = 11.2	46	2.466±.008	3.27±.23
22	2.918±.007	2.50±.17	49	.116±.011 R = 10.5	46	2.802±.009	3.29±.23
5	2.812±.010	2.74±.25	27	.131±.017 R = 7.7	33	2.681±.014	4.59±.38
4	4.216±.009	1.59±.14	28	.133±.017 R = 7.8	32	4.083±.014	2.86±.24
23	3.535±.008	1.67±.15	28	.137±.014 R = 9.9	31	3.398±.011	2.66±.23
25	5.801±.016	2.57±.19	41	.395±.019 R = 20.8	48	5.406±.010	2.56±.18
24	6.647±.014	1.97±.15	41	.028±.019 R = 1.5	48	6.619±.013	2.76±.19
2	4.037±.012	2.48±.21	32	.073±.019 R = 3.8	41	3.964±.015	3.56±.27
11	2.961±.011	2.86±.26	27	.048±.017 R = 2.8	33	2.913±.013	3.87±.32
mentum + ligula	3.578±.013	2.56±.27	21	.009±.031 R = 0.3	21	3.587±.028	5.28±.55
Hooks	20.22 ±.20	9.76±.69	45	.61 ±.33 R = 1.8	48	20.83 ±.26	12.00 ±.87
5:11	95.02 ±.44	3.56±.33	27	2.92 ±.69 R = 4.2	33	92.10 ±.53	4.88 ±.40
4:11	142.40 ±.45	2.47±.22	28	2.12 ±.80 R = 2.65	32	140.28 ±.66	3.95±.33
23:11	119.42 ±.42	2.79±.25	28	0.77 ±.71 R = 1.1	31	118.65 ±.59	4.13±.35
25:24	87.29 ±.26	2.78±.21	41	5.58 ±.35 R = 15.9	48	81.71 ±.23	2.89±.20
2:24	60.80 ±.22	3.03±.25	32	.71 ±.33 R = 2.1	41	60.09 ±.25	4.03±.30

strains with a very light coloration of the abdomen; this demand determined the appearance on the market of the "three banded" bees called also "golden" bees.

While working in the apicultural laboratory of Cornell University, through the help and courtesy of Prof. Phillips and various beekeepers scattered over the United States, we had the opportunity to study the bee races cultivated in this country. For tongue measurements we decided to have 50 bees from each separate apiary, taking them from ten colonies. For measuring other characteristics bees were taken from four apiaries (two in Ohio and two in Alabama). Starting our discussion with the tongue length we see from Table 18 that the yellow bees have considerably longer tongues than the black ones. Remembering the rôle of geographical variation of the bee tongue in Eastern Europe we attempted to put the obtained averages on the geographical map (see Fig. 12). It turned out that there are no indications of a smaller size of tongue in American yellow bees in the northern parts of the country. It would be indeed unreasonable to expect such a rule if we remember how many queens are sent every year from the southern to the northern states. According to some estimations not less than 500,000 queen bees are sold every year by queen breeders to the beekeepers in the United States, and it is mostly in the South that the breeders have their apiaries for commercial queen breeding.

TABLE 18

Average tongue lengths and coefficients of variation of bees of different races cultivated in the United States of America

	LOCALITY		MEAN IN MM.	COEFFICIENT OF VARIATION
Italian bees	1	Pennsylvania	6.324±.009	1.55±.10
	2	Kentucky	6.166±.011	1.78±.12
	3	Alabama (apiary I)	6.332±.010	1.73±.12
	4	Alabama (apiary II)	6.340±.010	1.63±.11
	5	Ohio (apiary I)	6.419±.012	2.00±.14
	6	Ohio (apiary II)	6.396±.013	2.05±.14
	7	Ithaca, N. Y.	6.224±.012	2.00±.14
	8	New York	6.388±.010	1.69±.11
Black bees	1	Ontario	5.960±.013	2.27±.15
	2	North Carolina	5.869±.009	1.69±.11
	3	Florida	5.974±.007	1.29±.09
Gray Caucasian bees	1	Colorado	6.638±.009	1.53±.09

The black bees we succeeded in measuring from three localities in this country give a very similar length of tongue. They also do not show any geographical regularity comparable with that exhibited by bees in Eastern Europe. We suspected at the beginning of our work on American bees that black bees in this country would show some differences in the North and in the South. It seemed easy to imagine that the black bees imported for years into the United States would have been differentiated according to natural conditions in the South and in the North. But this is probably not the case. Figure 13 represents graphically the variation of the tongue length of bees measured in the

United States of America. The four curves below show that the variability of the tongue length of the American Italian bees is not uniform in different apiaries. For instance, the apiary from Kentucky gives only 6.166 ± .011 mm. and the two apiaries from Ohio show the highest length—6.419 ± .012 and 6.396 ± .013 respectively.

calculate the average tongue length, which is equal to 6.428 ± .005. Specimens of Italian bees reared from queens imported from Northern Italy were sent to us from Caucasus. The material was preserved in a dry condition and we have been obliged to select for measurement only specimens with well stretched ligula. The average so obtained is 6.298 ± .015,

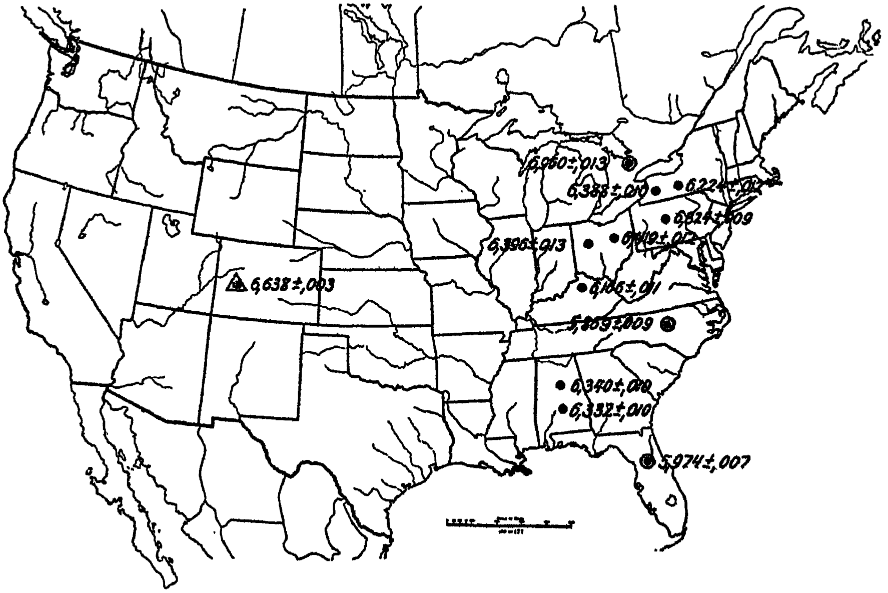

FIG. 12. MAP OF THE UNITED STATES REPRESENTING THE AVERAGE TONGUE LENGTH OF BEES BELONGING TO DIFFERENT RACES AND DIFFERENT APIARIES

The numbers below 6.00 mm. refer to the black bees (dots in a circle), the average in Colorado to the gray Caucasian bees (triangles). All others represent the yellow Americanized Italian bee.

Comparing the tongues of the Italian bees reared in the United States with native Italian bees, which gave us the tongue length equal to 6.234 ± .010 mm., we observe that some of the American apiaries show a longer tongue than the Italians and one apiary (Kentucky) on the contrary a shorter one. We do not have at our disposal material enough to reach a sound conclusion concerning the tongue length of true Italian bees. Chochlov's measurements based on Italian bees from three colonies ($N = 300$) permit us to the bees belonging to seven colonies. Summing up our whole experience we conclude that the average tongue length of different strains of Italian bees varies from 6.15 to 6.45 millimeters.

In regard to other characteristics of Americanized bee races we have to turn our attention to the tables containing summarized data on all bee races (Tables 16–21).

Table 19 shows that the American Italian bees compared with Russian bees (55° and 50° of latitude) have shorter wings, but practically the same width of wing. The index 25:24 is the same in American Italian and in Russian bees. On the other hand, the width is larger in American Italian than in Russian bees.

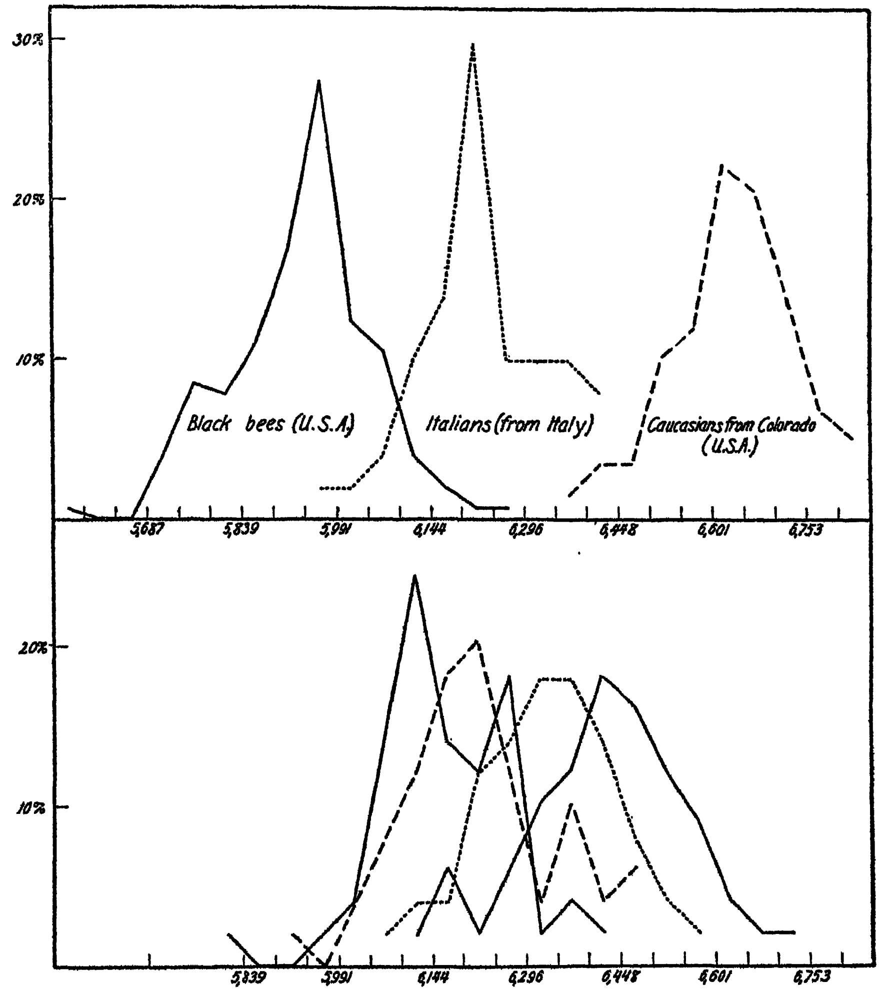

FIG. 13. VARIATION CURVES OF TONGUE LENGTH OF DIFFERENT RACES

Four lower curves show the variation of the tongue of bees from Kentucky, Ithaca, Alabama and Ohio. The frequencies are given in percent.

American Italian bees compared with Italian bees from Italian queens have larger wings in absolute dimensions (the R for the differences in the width is only 3.8) and relatively narrower wings, being in that respect intermediate between the Italian born from Italian queens and black Russian and Ukrainian bees.

If we compare the American Italian with American black bees we find between them a difference of almost the same value as between the black and Italian bees in Europe. The American black bees have longer wings (the probable error ratio is only 3.3 for the proximal length) and

TABLE

Biometrical constants of wing measurements and proportions

		BLACK BEES			ITALIAN BEES		CAUCASIAN BEES					
		M. Russia	S. Russia	U. S. A.	U. S. A.	Italy and Caucasus	North Caucasus	Abchasia	Central Mountains	Delidjan	Migri	Colorado U. S. A.
24	M	4.913±.002	4.871±.003	4.843±.008	4.813±.004	4.735±.006	4.792±.004	4.833±.006	4.846±.007	4.852±.013	4.685±.016	4.872±.010
	C	2.10±.03	2.18±.05	2.89±.12	2.37±.06	1.78±.09	2.03±.06	2.38±.08	2.13±.10	2.40±.18	2.35±.24	2.27±.14
	N	893	451	128	360	87	241	182	95	37	22	56
25	M	4.553±.002	4.499±.003	4.506±.006	4.448±.004	4.351±.008	4.398±.003	4.469±.005	4.511±.008	4.482±.009	4.440±.010	4.547±.008
	C	2.10±.03	2.34±.05	2.09±.09	2.24±.06	2.44±.12	1.80±.06	2.15±.08	2.32±.12	1.80±.14	1.54±.16	1.85±.12
	N	887	449	128	360	87	241	182	95	39	22	56
2	M	3.166±.002	3.189±.003	3.131±.004	3.177±.003	3.154±.005	3.071±.004	3.146±.004	3.166±.006	3.162±.009	3.158±.010	3.236±.005
	C	2.19±.04	2.43±.05	2.16±.09	2.29±.06	2.37±.12	2.14±.09	2.53±.09	2.71±.13	2.63±.21	2.11±.21	1.84±.12
	N	875	449	128	360	87	137	182	95	37	22	56
Index 25:24	M	92.68±.05	92.39±.08	93.08±.17	92.44±.09	91.91±.16	91.67±.10	92.50±.13	93.04±.17	92.40±.21	94.81±.28	93.37±.21
	C	2.32±.04	2.77±.06	3.02±.13	2.60±.07	2.41±.12	1.92±.08	2.72±.10	2.51±.13	2.04±.16	1.98±.20	2.47±.16
	N	887	449	128	360	87	141	182	86	37	22	56
Index 2:24	M	64.46±.03	65.47±.05	64.67±.10	66.03±.06	66.62±.12	64.50±.07	65.11±.07	65.34±.11	65.18±.14	67.43±.23	66.45±.13
	C	2.26±.04	2.52±.06	2.54±.11	2.39±.06	2.39±.12	1.93±.08	2.23±.08	2.53±.12	1.94±.15	2.39±.24	2.25±.14
	N	875	449	128	360	87	137	182	95	37	22	56

TABLE 20

Biometrical constants of hind leg measurements and proportions

		BLACK BEES		ITALIANS		CAUCASIANS				
		55° M. Russia	50° S. Russia	U. S. A.	Italy	North Caucasus	Abchasia	Central Mountains	Migri	Colorado U. S. A.
5	M	2.125±.004	2.095±.004	2.102±.004	2.081±.005	2.116±.005	2.087±.003	2.095±.004	2.058±.006	2.112±.004
	C	2.54±.14	2.45±.13	2.59±.12	2.70±.18	3.19±.15	2.42±.12	2.93±.14	2.40±.22	2.13±.13
	N			99	49	97	98	94	27	60
4	M	3.363±.006	3.293±.005	3.276±.005	3.225±.005	3.438±.005	3.421±.004	3.405±.005	3.314±.008	3.439±.005
	C	2.26±.13	2.02±.11	2.03±.10	1.74±.12	1.94±.09	1.75±.08	2.24±.11	1.89±.17	1.68±.10
	N			99	49	97	98	94	27	60
23	M	2.738±.004	2.678±.004	2.682±.005	2.653±.005	2.777±.004	2.741±.003	2.750±.004	2.669±.006	2.724±.003
	C	1.72±.09	2.09±.11	2.50±.12	1.78±.12	1.93±.09	1.76±.08	2.23±.11	1.69±.16	1.42±.09
	N			99	49	97	98	93	27	60
5:11	M	90.69±.24	92.55±.26	93.20±.23	95.89±.33	93.79±.21	91.77±.15	91.40±.22	92.74±.23	93.50±.23
	C	3.38±.19	3.64±.30	3.66±.18	3.53±.24	3.34±.16	2.38±.11	3.47±.17	1.88±.17	2.79±.17
	N			99	49	97	98	94	27	60
4:11	M	143.48±.36	145.44±.41	145.24±.34	148.61±.45	152.40±.24	150.46±.23	148.51±.28	149.35±.55	152.22±.27
	C	3.22±.18	3.62±.20	3.47±.17	3.16±.21	2.30±.11	2.20±.10	2.73±.13	2.85±.26	2.01±.12
	N			99	49	97	98	94	27	60
23:11	M	116.81±.23	118.30±.32	118.88±.27	122.25±.38	123.10±.21	120.54±.18	119.93±.23	120.98±.51	120.59±.26
	C	2.45±.14	3.49±.19	3.40±.16	3.21±.22	2.49±.12	2.20±.10	2.80±.14	3.29±.30	2.47±.15
	N			99	49	97	98	93	27	60

TABLE 21

Biometric constants of abdomen measurements and proportions

		BLACK BEES		ITALIANS		CAUCASIANS				
		55° M. Russia	50° S. Russia	U. S. A.	Italy	North Caucasus	Abchasia	Central Mountains	Migri	Colorado, U. S. A.
8	M	2.453±.004	2.387±.005	2.385±.004	2.306±.005	2.391±.004	2.390±.005	2.406±.004	2.341±.007	2.380±.004
	C	1.86±.13	2.30±.16	2.36±.11	2.05±.14	2.49±.12	2.21±.14	2.26±.11	2.22±.20	1.96±.12
	N			98	48	98	59	95	27	59
21	M	1.778±.005	1.632±.006	1.628±.005	1.511±.005	1.589±.004	1.633±.003	1.670±.004	1.610±.006	1.654±.005
	C	2.65±.18	3.75±.27	4.26±.21	3.47±.24	3.72±.19	2.90±.15	2.98±.15	2.86±.27	3.28±.21
	N			92	46	90	86	85	26	56
22	M	2.988±.007	2.858±.007	2.861±.005	2.732±.006	2.830±.005	2.855±.005	2.884±.005	2.789±.010	2.823±.007
	C	2.22±.14	2.45±.17	2.71±.13	2.13±.15	2.41±.12	2.27±.12	2.56±.13	2.64±.25	2.72±.17
	N			92	46	90	86	85	26	56
21:22	M	59.53±.12	57.10±.13	56.91±.13	55.31±.15	56.15±.11	57.18±.09	57.92±.11	57.75±.24	58.59±.11
	C	1.99±.14	2.25±.16	3.16±.16	2.73±.19	2.85±.14	2.27±.12	2.64±.14	3.13±.29	2.17±.14
	N			92	46	90		85	26	56
10	M	2.541±.006	2.423±.008	2.431±.005	2.302±.006	2.390±.005	2.365±.005	2.393±.005	2.337±.007	2.405±.008
	C	2.49±.17	3.29±.23	3.14±.16	2.83±.20	2.69±.13	2.66±.14	2.79±.15	2.03±.20	2.78±.18
	N			92	46	91	87	77	23	56
26	M			1.756±.021	1.076±.021	.8116±.0174	.7188±.0159	.5054±.0132	1.297±.040	.5961±.0164
	C			17.71	20.71	31.29	32.42	35.36	23.68	31.54
	N			99	49	97	98	84	27	60
11	M	2.345±.005	2.266±.006	2.257±.005	2.172±.007	2.257±.004	2.274±.004	2.293±.005	2.220±.007	2.260±.005
	C	2.93±.15	3.24±.18	3.12±.15	3.27±.22	2.61±.13	3.52±.12	2.99±.16	2.31±.21	2.50±.15
	N			99	29	97	98	84	27	60
26:11	M			77.74±.91	49.50±.91	35.90±.76	31.62±.70	22.32±.59	58.52±1.82	26.40±.73
	C			17.34	20.10	11.14	32.55	35.68	24.02	31.76
	N			99	49	97	98	84	27	60

absolutely and relatively narrow wings. The black American bees have to be placed not far from the type of the Ukrainian bees in respect to the characters of the wing, having even a shorter distal length.

Table 20 contains data on variation of the hind legs. The absolute size of the leg joints of American Italians is smaller than in Middle Russian bees (for the difference in the first joint of the tarsus the probable error ratio is only 3.8). In respect to the absolute and relative size of the leg joints the American Italians practically agree with the Ukrainian bees. In harmony with a larger size of wings the American Italians have also longer joints of the hind legs than the Italians from Italian queens. The latter are definitely more long legged (according to the indices) than the American Italian bees.

The biometrical constants and the results of comparison of different races in respect to the characters measured on the abdomen are represented in Table 21.

The American Italians compared with Middle Russian bees show that all abdominal characteristics are smaller in size in the former group. The American Italians have practically the same size of abdomen as the Ukrainian bees, being therefore larger than Italian bees from Italy. In regard to the index of the wax gland the American Italians correspond perfectly to the Ukrainian bees, being just between the Middle Russian and Italians from Italy.

Concerning the coloration of the third band of the abdomen the yellow band is definitely larger in the American Italians than in the Italians from Italy. The scheme of coloration in figure 14 shows that, among the bees studied, the American Italians represent the lightest colored type of bees. It is evident that this is the result of an artificial selection in the direction of the production of light colored golden bees.

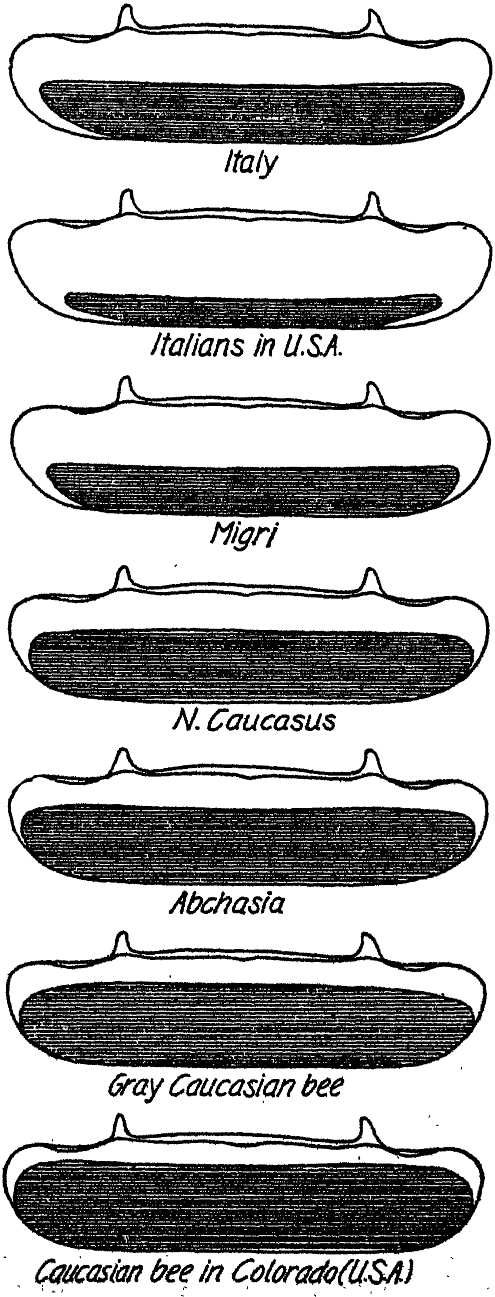

Fig. 14. Scheme of Coloration of the Third Tergum of Italian and Caucasian Bees Based on Actual Average Measurements of the Yellow Stripe

CAUCASIAN BEE RACES

Turning our attention to the variation of the bees in the south-east corner of Europe and in Caucasus it must be said that the situation here is more complicated. This is due to two probable groups of causes. First, the Caucasus is zoogeographically divided into several sharply limited regions with peculiarities in the composition and the origin of the organic life. Secondly, in Caucasus we have to deal not only with a change of climatic conditions on the plain but also with a change which occurs with elevation on the mountain chains. The first observation of the differentiation of the Caucasian bees in groups has been made in regard to the coloration of the abdomen.

According to Gorbatschev (see the map in Fig. 15 taken from his article, (26)) the Central chain of the Caucasian mountains is populated by gray Caucasian bees, which he describes under the name of *Apis mellifera caucasica* Gorbatschev.

Another distinct form is the so-called yellow Persian bee inhabiting Lenkoran and some regions of Armenia and Azerbeijan. The northern Caucasus prairies and the hills in Transcaucasia are populated by a bee of an intermediate type—hybrids according to Gorbatschev's interpretation. We combined our material from Caucasus in groups according to the origin, i.e., locality. In our article on hooks (11) we included the bees from Migri representing true yellow Persian bees in the

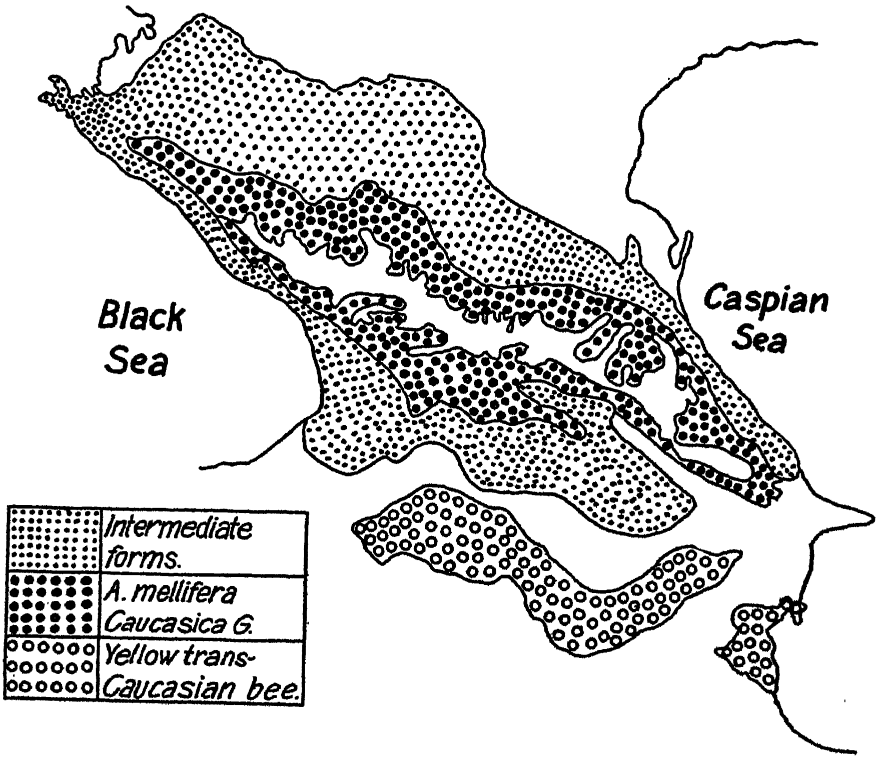

FIG. 15. MAP OF CAUCASUS SHOWING THE DISTRIBUTION OF DIFFERENT VARIETIES OF BEES (After A. Gorbatschev, 1916)

same group with those from Delijan which are according to our later investigation on coloration quite different from them, being very close to gray Caucasian bees. Bees from Tiflis, Swanetia and Kutais we consider as true *Apis mellifera caucasica* Gorbatschev. The bees from apiaries on the eastern coast of the Black Sea (see our map, Fig. 9) we shall treat separately, being informed that the bees from this region (Abchasia and adjacent localities) differ from the gray Caucasian bees of the Central chain in respect to different peculiarities of their behavior and biology. Bees sent to us from Stavropol and Maikop have been specified as North Caucasian bees, although the Maikop bees are, it seems, a link between these and Mountain gray bees. We had also the opportunity to investigate Caucasian bees cultivated in the United States in Colorado.

In Table 22 are presented data from different sources relating to the tongue length of Caucasian bees. The largest material comes from Tiflis, where a state apiary has been selling queens of the Caucasian gray bee for many years. The apiary was under the supervision of K. A. Gorbatschev. It seems that the length of the tongue of Tiflis and Abchasian bees (Gagri, Adler, Kichmai) lies between the limits of 6.60 and 6.70 millimeters. An insufficient number of colonies or a lack of proper precautions in collecting the material does not allow us to draw any definite conclusion about the deviation of other Caucasian bees from gray ones. The North and Transcaucasian bees must have an average tongue length in no case below 6.500 millimeters. Further investigation will be necessary to clear up this question.

Turning our attention to other characters we see that both wing lengths show that the Caucasian bees are smaller than Middle Russian ones. Compared with Ukrainians we see that only North Caucasus, Abchasian, and Migri bees show statistically significant differences, the bees from the Central Mountains and Delijan being practically of the same size in both lengths (24 and 25). The absolute width of the wing does not give a very clear picture. The wings of the North Caucasus bees are exceptionally narrow, other Caucasian bees having the same absolute width as the Middle Russian bees. The index 25:24 continues a decrease southwards which was begun by Ukrainian bees, then increases again in Abchasian, Central Mountains and Delidjan bees and reaches a very high value in Migri bees, 94.81 ± .28. The relative width of the wings is, with the exception of North Caucasian bees, higher than in Middle Russian ones, having an extremely high value in Migri bees. The Colorado bees are in their coloration very close to the gray Caucasian mountain bees and differ from them only in absolutely and relatively broad wings.

The absolute size of the tarsal joint does not give a very clear picture, being in some groups of the Caucasian bees smaller than in Middle Russian ones and in others practically equal to them. The variation of the tibia is quite remarkable. This joint is *larger*, in all except Migri bees, than in Middle Russian and naturally in Ukrainian bees. The femur is, as compared with Middle Russian bees, larger in North Caucasus and smaller in Migri bees. The relative length of the legs is larger than in Middle Russian bees as shown by all the indices. Particularly pronounced is the difference in the relative length of the femur. The ratios showing the statistical differences of the proportion of the first tarsal joint are not significant in the cases of Abchasian and Caucasus Mountain bees. The Colorado Caucasians have absolutely longer tarsal joints than

TABLE 22

Tongue length of Caucasian worker bees from different localities (Data collected from different sources)

ORIGIN OF THE MATERIAL OR RACE	PLACE OF DEVELOPMENT	NUMBER OF COLONIES	NUMBER OF SPECIMENS	MEAN	COEFFICIENT OF VARIATION	HOW COLLECTED	AUTHOR
Gagri (Abchasia)	Orel district (Middle Russia)	3	300	6.731±.007	2.64	Boiling water, etc.	Chocklov, 1918
Kars (W. Transcaucasia)	Orel district (Middle Russia)	3	300	6.642±.005	2.02	Boiling water, etc.	Chocklov, 1918
Tiflis	Tiflis	3	150	6.602		Collected in boiling water and sent in 2% formalin	Michailov, 1927
Tiflis	Nizhni Novgorod	4	379	6.670±.004	1.71±.04	Boiling water	Kurotschkin, 1928
Tiflis	Tiflis	5	154	6.658±.006		Boiling water, etc.	Michailov, 1928
Kuban (N. Caucasus)	Kuban	3	50	6.531±.013		Boiling water, etc.	Michailov, 1926
Kichmai (Sotchi-Tuapse W. Caucasus)	Kichmai	10	39	6.621±.016		Tongue carefully stretched out	Alpatov, 1928
Adler (W. Caucasus)	Adler	13	58	6.653±.010		Preserved in dry condition	Alpatov, 1928
Gray Caucasian bee	Colorado (U. S. A.)	10	circ. 50	6.638±.009		Boiling water, etc.	Alpatov, 1928
Maikop (N. Caucasus)	Maikop	more than 8	19	6.539±.031		Collected dry without any precautions	Alpatov, 1928
Delidjan (Transcaucasus)	Delidjan	4	29	6.509±.020		Collected dry without any precautions	Alpatov, 1928
Migri (Transcaucasus)	Migri	3	13	6.511±.020		Collected dry without any precautions	Alpatov, 1928

Abchasian, absolutely larger tibia than Caucasus Mountain bees, and shorter femur than dark bees from Caucasus. The indices in Colorado Caucasians show very high values, even in more pronounced form than in dark bees from Caucasus.

Examining the characters on the abdomen we can establish two rules: the first is that all Caucasian bees are smaller than the Middle Russian. Some of them are smaller than the Ukrainian, while some are practically equal in size to the latter. Only the 10th and 8th measurements are exceptions to the following serial change in abdomen measurements: North Caucasus < Abchasia < Central Mountains> Migri.

The proportions of the wax sternum show in general that the Caucasian bees have a smaller wax gland than the Middle Russian; the relationship of Caucasian bees is as follows: North Caucasus < Abchasia < Caucasus Mountains = Migri.

The Caucasians from Colorado are near the Abchasian bees in respect of the abdominal measurements, being in some of them a little smaller than the gray Caucasian bees from Caucasus.

The coloration of Caucasian bees presents no difficulties in interpretation. The gray Caucasian bees from the Caucasus Mountain chain are the darkest, the opposite end of the series being occupied by Migri bees. The Colorado Caucasians do not differ significantly from those of the Caucasus Mountains. The Abchasian and North Caucasian bees are closely related, having a large percentage of yellow color on the third tergum.

The last relationship that we have to discuss is that of yellow Caucasian bees to Italians. We shall compare them only with Italians bred in Italy and from queens imported from Italy. It seems very probable that the tongue length of North Caucasian and Migri bees is greater than that of Italian bees. The Italians, judging from the whole experience, have a tongue length varying in different apiaries from 6.15 to 6.45. The North Caucasian bees have an average tongue length at least not less than 6.50 millimeters. The North Caucasian bees are larger than the Italians in regard to all the absolute measurements. There is a pronounced difference between them in that the Caucasian bees have a narrower form of the wing (2:24). The Italians have relatively large first joints and short tibias. The coloration of the third tergum is much lighter. The Migri bees have also nearly all absolute measurements larger than those of the Italian bees (exceptions are the following characters: 24 where $R = 2.9$, 5 where $R = 3.3$, and 23 where $R = 2.0$). The coloration of Migri bees is even lighter than that of the bees from Italy. Wings have a high value of the indices 2:24 and 25:24. The relative length of the first tarsal joint is larger in Italian than in Migri bees. Both groups of Caucasian bees have a larger wax gland index than the Italians ($R = 4.4$ and 8.7). It seems that both groups of yellow Caucasian bees differing from the Italians have some peculiarities linking them with other Caucasian bees (longer tongue, larger size of the body and of the wing). The definite conclusion is that the Caucasian yellow bees have to be considered as a strain of southern bees independent of the yellow Italian bees—*Apis mellifera ligustica* Spinola.

HEREDITARY CHARACTER OF RACIAL DIFFERENCES IN BEES

The racial differences which have been described above as occurring in bees belonging to different parts of the area of distribution of species of *Apis mellifera* L. raise the question of their hereditary nature. Unfortunately nothing is known about the heredity of the honey bee. This is due to the difficulties of controlling the mating of the queens, which takes place in the air. Up to the present time all the attempts to mate the queen indoors have failed. Quite recently Watson (80, 81) developed a very delicate technique for the instrumental insemination of the queen. Without doubt this method will help very much to investigate thoroughly the genetics of one of our domesticated animals.

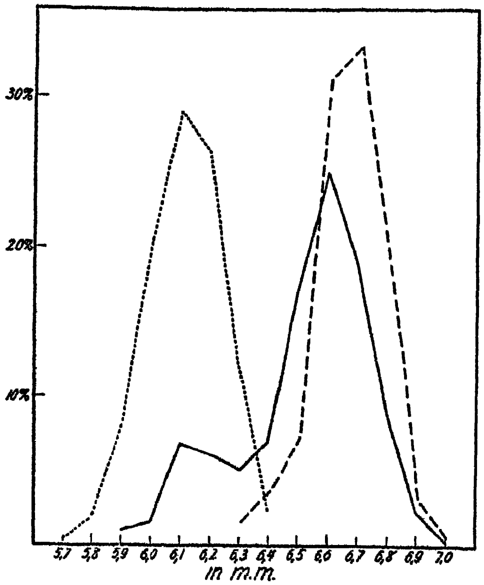

FIG. 16. VARIATION CURVES OF THE TONGUE LENGTH OF GRAY CAUCASIAN BEES REARED IN MIDDLE RUSSIA AS COMPARED WITH MOSCOW BEES (DOTTED LINE)

Continuous line represents the variation of worker bees collected from nine colonies where the Moscow queens were replaced by gray Caucasian queens. The dash line shows the variation of bees from four colonies of gray Caucasian bees cultivated in Nizhni Nowgorod. The frequencies have been calculated in percents.

We propose now to bring together a few of the facts relating to the inheritance of racial differences in the honey bee. One of the oldest facts is the observation of Dzierzon of the transmission of color in a cross of the black and the yellow Italian bees. These observations gave origin to the discovery of the parthenogenetic nature of the drones. A recent publication of Newell (59) shows that the color is inherited as a Mendelian character. Besides that, the stability of the racial differences in color has been proved hundreds of times in observations of the progeny of the queens of yellow races imported to the north. From this point of view the transportation of different strains of the honey bee to the United States represents in itself a great experiment. The differences found by us between the yellow and the black bees in the United States, which are of the same sense and direction as the differences between the Northern and Southern European bees, furnish a direct proof of the stability of these racial characteristics. The same is true of the Caucasians cultivated in the United States of America. We have seen that in their constitutional characteristics they remain extremely closely related to the ancestral stock. Through the courtesy of A. F. Gubin, Director of the Moscow Apicultural Experiment Station, we possess some data illustrating the inheritance of the tongue length of Caucasian bees in Middle Russia. Figure 16 represents variation curves of the native Moscow bees (dotted line) and bees produced by gray Caucasian queens introduced into Moscow colonies (continuous line). The Moscow curve is based on measurements of 1000 bees taken from ten colonies, the Caucasians on measurements of 900 bees from nine colonies. The bees were measured a few weeks after the requeening of the Moscow colonies (nine) by Caucasian queens. Not all the Moscow worker bees had been replaced by workers emerged from the brood of Caucasian queens; the left summit in the Caucasian curves represents the remaining Moscow bees. The dash line shows the variation curve of four colonies of Gray Caucasian bees produced by Caucasian (Tiflis) queens sent to Nizhni Novgorod (Middle Russia). We can see that the progeny of Caucasian bees developed in Middle Russia has approximately the same length of tongue as the Caucasian gray Mountain bees (6.60–6.70 mm.). Another example is a transportation of four colonies of bees from the Kursk district to Moscow. Measuring the tongue length of three Moscow colonies and of the colonies brought the year before from Kursk (let us call them Ukrainians), we get the following average length of tongue for the two groups under consideration: Moscow 6.038 ± .016, Kursk 6.321 ± .010, Diff. = .283 ± .018, Ratio = 15.7. Kursk is situated 4° south of Moscow and according to our formula we should expect there bees with a tongue length 0.302 mm. longer than in Moscow. This figure is not far from the difference obtained above. Figure 17 shows the curves of the bees of Kursk and native Moscow ones. Measurements of other characters showed a slight approach of the Ukrainian bee to the type of Ukrainian bee established above—smaller size of body, of the wings, and of the legs, and a larger number of hooks. But owing to the small number of cases, the large probable errors do not permit us to affirm positively that Ukrainian bees transported to the North preserve a southern constitutional type. This is one of the most important problems to be further investigated in the future.

We cannot omit to mention a paper of Michailov (53) in which the author attempts to compare the offspring of the Caucasian queens developed in Tiflis (Caucasus) and in Tula (Middle Russia). Queens which had already wintered once were sent from Tiflis to Tula and introduced there into hives with brood and not field bees. Special care was taken to send the queens accompanied by their own offspring, which were used to characterize the Caucasian bees born in Caucasus. In two months after the arrival of Caucasian queens a collection of bees from their hive was made. The bees were collected during their emergence so that it is safe to say that they represent the offspring of the Caucasian queens. In this way offspring of five queens has been investigated. Table 23 represents the absolute measurements and they confirm the conclusion reached above regarding the north-south variation in the constitution of the bee body.

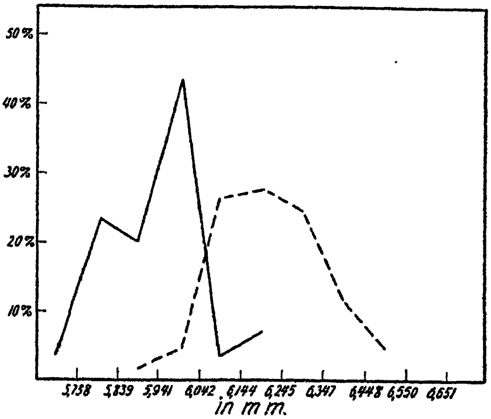

Fig. 17. Variation Curves of the Tongue Length of Native Moscow Bees and Bees from Colonies Transported to Moscow from the South

The continuous line represents bees taken from three colonies of native Moscow bees. The dotted line is based on measurements of bees from four colonies which one year before were transported to Moscow from a southern locality (Kursk District). The frequencies are expressed as percents.

The range of variation of the tongue index is from 126.7 to 129.0 for bees on the plain of European Russia (Leningrad, Tula). For the Caucasian bees this index has a quite different range, namely 145–148. The wing index for Russian bees is less than 200, for Caucasian bees it is above 200. The wings are broader in Caucasian bees. The Caucasian bees born in Tula remain within the limits characteristic of Caucasian bees in regard to the proportions of the body. The reduction of the tongue and wing measurements in Tula offspring of the Caucasian bees is not in accord with the observations of Chochlov, Kurotchkin, Gubin and our own measurements. It seems to us that the only probable explanation is that in Michailov's case the queens were introduced not in normal colonies but in hives with young brood and young bees. We have seen above that there is a certain influence of the age of the nurse bees on the reduction of the bee body in size. In both cases the strength and the normal composition of the bee colony were disturbed, which had as a consequence a

TABLE 23

Biometrical constants of Caucasian worker bees born in Tiflis compared with their sisters produced by the same mothers shipped to Middle Russia (Tula)

(From Michailov, 1928)

	154 BEES FROM 5 COLONIES: BORN IN TIFLIS	DIFFERENCE AND $R = \frac{\text{DIFF.}}{\text{P.E.}}$	490 BEES FROM THE SAME QUEENS: BORN IN TULA
Tongue	6.658±.005	.166±.008 R = 20.7	6.492±.005
	1.61 ±.06		2.78 ±.06
Length of wing	9.226±.008	.076±.009 R = 8.4	9.150±.004
	1.57 ±.06		1.60 ±.03
Width of wing	3.153±.004	.030±.004 R = 7.5	3.123±.002
	2.31 ±.09		2.39 ±.05
Hooks	21.73 ±.11	.47 ±.12 R = 3.9	21.26±.06
	9.52 ±.37		8.60 ±.19
Tergum (III + IV)	4.461±.006	.024±.008 R = 3.0	4.485±.005
	2.34 ±.09		3.70 ±.08
Tongue: tergum (III + IV)	149.32 ±.21	4.39 ±.28 R = 15.7	144.93±.19
	2.65 ±.10		4.31 ±.09
Length of wing: tergum (III + IV)	206.91 ±.29	2.64 ±.37 R = 7.1	204.27 ±.23
	2.54 ±.10		3.72 ±.08
Width of wing: length of wing	34.18 ±.03	.27 ±.04 R = 6.75	33.91 ±.02
	1.87 ±.07		1.93 ±.04

decrease in size of different parts of the body of the bees, although in the first and in the second case different parts of the body were not influenced in an identical way.

In any case the whole bulk of the material on the transportation of bee races to new localities shows that the characteristics are inherited. They cannot be considered as purely phenotypical phenomena.

BIOLOGICAL DIFFERENCES OF BEE RACES

It is beyond the plan of the present paper to bring together the tremendous number of observations scattered through the beekeeping literature of every country in the world concerning the racial differences in the behavior and productiveness of the honey bee. The most important defect in all such results is that they are usually based on the observation of a comparatively restricted number of cases. We have shown above that a bee colony can be very easily described by a number of physical characteristics. The same is true in respect to the biological characteristics. This fact is known to everybody who has occasion to handle bees. This highly developed individuality of bee colonies prevents us from drawing conclusions about racial differences unless a large number of colonies of races under comparison are examined. As a rule this is rarely fulfilled. In many cases of racial description we are doubtful as to whether the observed differences are to be considered as real differences between the races under comparison, or as chance deviations of a few colonies with imported queens from the colonies with native bees. The second point is that the racial differences in biological characteristics as well as in morphological ones are usually of a quantitative character, the variation being transgressive. Consequently it is highly desirable to have a numerical expression of the biological characteristics. Unfortunately at the present time methods for quantitative observations of bee behavior are almost entirely wanting. The only attempt to use exact measurements in characterizing one of the most important features of comparative queen biology has been made by Nolan (60) in his brood rearing investigations.

It seems to us that at the present time the comparative and quantitative survey of the biology of different bee races is one of the most important questions in the natural history of the honey bee, from the theoretical as well as from the practical point of view. Our intention is to give here only a few examples of biological differences between races of bees.

On the plain of European Russia, which is occupied by a black variety of *Apis mellifera*, we have shown a gradual change in morphological characteristics in the southern direction. This is accompanied by some changes in swarm instinct. The first (or prime) swarm is a group of bees leaving the colony with the old queen after the sealing of the queen cells. For the Middle Russian bee (Briuchanenko, 21) and the German bee (Zander, 84) that event takes place on the same day or on the next day after the sealing of the first queen cell. In the Ukrainian bee (Southern Russia) this happens only on the third day and for the Crimean bees (farther south) the bees do not swarm before the sixth to eighth day.

Among the Ukrainian bees cases of occurrence of two queens in one hive have been reported oftener than among the Middle Russians. For North Caucasian bees, according to the observation of beekeepers, sometimes thirty per cent of the colonies have two queens who are peacefully living together, a picture which is unfamiliar to a beekeeper in northern and southern Russia.

The number of after swarms produced in different races is very variable. A. I. and E. R. Root (69) write evidently about the Italian bee cultivated in the United States of America: "All swarms that come out after the first swarm, or are led by a virgin queen or a plurality of them are generally termed after-swarms; and all swarms after the first are accompanied by such queens. There may be from one all the way up to a half dozen swarms." Nearly the same limit of the number of swarms is usually indicated for the Middle Russian bee. The yellow Caucasian bees according to Gorbatschev (26) are excessive swarmers, having sometimes twelve swarms per colony. On the other hand the gray mountain bees have a lower swarm instinct, approaching in that respect the bees from northern localities. A. and E. Root in their book (69) do not make any distinction between the yellow and gray bees from Caucasus. They write (*loc. cit.*, p. 715) about Caucasians in general. The most serious objection to them is their propensity to swarm. It is even more pronounced than in Carniolans.

Peculiarities in the development of the swarming instinct may characterize races of bees of a very limited territory. It has been reported that the bees of the Lüneburg marches in Germany are extreme swarmers. On account of this peculiarity they have been described under a special name as *A. mellifera Lehzeni* Buttel-Reepen (Buttel-Reepen, 20). An interesting characteristic of the Caucasian bee is a very high number of natural queen cells. The Middle European bee has, according to Berlepsch, 5–20 queen cells. The first exact number given by Koshevnikov (33) was 150 cells in a colony. Pickel recently indicated that the North Caucasian-Kuban bees have sometimes as many as 350 queen cells. Mosolevsky (58) reports that the Abchasian bees build very few queen cells, differing in that respect from the other Caucasian bees. In regard to the number of queen cells the Caucasian bee approaches the Egyptians (100–200 queen cells according to Buttel-Reepen) and Syrians (200–300 cells according to the same authority). Another peculiarity related to the reproductive functions which is developed in different degrees among races of the honey bee is the occurrence of egg laying worker bees (Koshevnikov, 33). Postojalko (67) indicated that the yellow Caucasian bees have more often egg-laying worker bees than the gray ones.

Turning our attention to the problem of differences of the bees belonging to different races in regard to their ability to collect nectar from different flowers, it may be pointed out that this particular question was just the starting point of the whole biometrical work on bee races. In the beginning of this century the Root Company claimed that its bees are able to collect nectar from the red clover—a plant which is not frequently visited by bees. The same question shortly before the world war was a subject of intensive investigation in Russia on the estates of one of the members of the royal family. I. N. Klingen (32), a broad minded agronomist, was the leader of these investigations and their practical application. He claimed to prove that the visiting of the red clover by bees depends on two circumstances: (1) the absence at the moment of the blooming of the red clover of any competition with other nectar secreting plants, (2) cultivation of long tongued bees (in his case Caucasian). Klingen was an ardent amateur of the gray Caucasian bees and several hundreds of Caucasian colonies were cultivated under his direction on the estates mentioned. His data show, with perfect evidence, that in the case where the clover was provided with a certain number of hives of Caucasian bees the crop of clover seed was much higher than in the case where these bees were absent.

The same question arose recently in Russia and became a subject of detailed investigation of several Apicultural Experimental Stations. We have the pleasure to acknowledge the permission of A. F. Gubin, Director of the Moscow Apicultural Experiment Station to publish the data obtained by him concerning the specific qualities of Middle Russian and Gray Caucasian bees. In the beginning of the summer of the year 1926 in nine colonies of the Moscow black native bees the queens were replaced by queens of the gray Caucasian bee sent from Tiflis (Caucasus). When the newly emerged Caucasian bees replaced nearly completely the Russian bees (see Fig. 16), samples of 100 bees were taken from these nine colonies as well as from ten other colonies with replaced Moscow queens. The variation curve for 1900 bees is represented on figure 18 by the continuous line. It is clear that the bimodal character of the curve is due to the presence of long tongued Caucasian worker bees with an average tongue length of about 6.60 mm. At the same time on the field of clover situated near to the apiary a collection of bees visiting the clover was made. The dotted line in Fig. 17 represents the variability of bees collected on red clover. Like the continuous line the dotted curve shows two peaks, one corresponding to the Moscow bees and the other to the Gray Caucasians. The most interesting fact is that in the dotted line the peak which represents the Middle Russian bees working on red clover is shifted a little to the right from the peak of Middle Russian bees collected from hives. It means that the Middle Russian bees which were collected during their work on red clover have a longer tongue than the general population of Middle Russian (Moscow) bees. In other words only comparatively long tongued bees are able to work on clover. The peak for Caucasian bees collected on clover does not show any shifting along the horizontal axis. This indicated that in the case of the Caucasians a selection of long tongued individuals did not occur. All Caucasian bees could work equally on red clover. We considered this discovery of A. F. Gubin as one of the most interesting facts concerning the relationship between the honey bee and flowers.

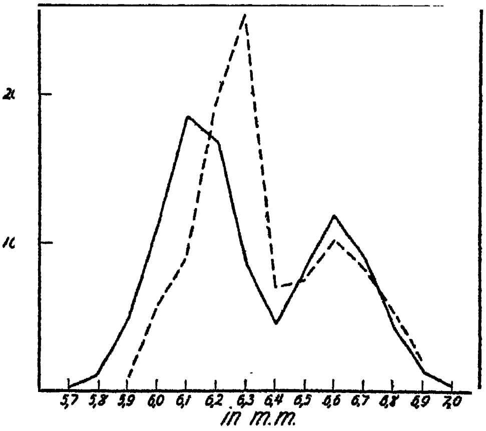

Fig. 18. Frequency Distributions of Tongue Lengths of Bees

The continuous curve shows the variation of the tongue length of 1900 bees taken from nineteen hives of the apiary of the Department of Apiculture of the Moscow District Agricultural Experimental Station. In 9 of these hives the Moscow native queens have been replaced by queens of the gray Caucasian race. The dashed curve represents the variation of 228 bees collected near to the apiary on flowers of red clover. The curves are based on data obtained through the courtesy of Dr. A. F. Gubin, Director of the Department of Apiculture.

Quite recently several attempts have been made to study the tongue length of bees collected from other honey plants. Table 24 presents data published by Gubin (29). It can be seen that the average length of the tongue of the bees collected on white clover and Swedish clover is smaller than that of bees collected on other plants.

TABLE 24

Average length of the tongue of the bees collected on different nectar producing flowers

(From Gubin, A. F., 1928)

	MEAN AND MEAN ERROR	
Fire weed	6.24±.01	
Vetch (*Vicia villosa*)	6.52±.01	
Red clover	6.22±.01	Rare visits
Red clover	6.22±.02	Mass visits
Red clover	6.30±.02	Mass visits
White clover	6.12±.01	
Swedish clover	6.14±.01	

Bees with extremely long tongues (evidently exclusively Caucasian) visited the vetch, while on the red clover there were working also Middle Russian bees, which lowered the average value of tongue length of the bees collected from this plant.

TABLE 25

Average length of the tongue of the bees collected on different nectar producing flowers

(From Kurotchkin, 1928)

	MEAN AND MEAN ERROR	TIME OF DAY	DATE	NO. OF SPECIMENS
Red clover	6.09±.02		23.7	36
Buckwheat	6.09±.02		1.8	46
Early Phacelia	6.20±.02		20.7	95
Late Phacelia	6.60±.02	6–7 a.m.	23.8	124
Late Phacelia	6.53±.02	7–8 a.m.	23.8	95
Late Phacelia	6.59±.02		23.8	50
Late Phacelia (bees with pollen mass)	6.35±.02		27.8	76
Late Phacelia (bees without pollen mass)	6.52±.02		27.8	89
Echum vulgare	6.14±.01		5.7	100

In Table 25 are represented analogous data collected by A. Kurotchkin in Nizhni Nowgorod. The apiary of the Nizhni Nowgorod Zootechnical Experimental Station contained, besides native bees, also several colonies of Caucasian bees from Tiflis. Gubin's and Kurotchkin's data are not comparable. The conditions of honey secretion in two different localities and different seasons of the year are so variable that at the present moment we are not able to draw very definite conclusions about the absolute requirements in tongue length necessary for work on such a plant as red clover. It is not apparent why the bees on red clover in Kurotchkin's measurements have such a short tongue as compared with the measurements of Gubin. In Table 25 the most striking fact is the highest value for the late *Phacelia* which evidently attracted mostly Caucasian bees. Another interesting point observed by Kurotchkin is that the bees collecting pollen show a pronounced difference in the length of the tongue from those collecting nectar. It means that among the bees engaged in pollen collecting the native short tongued individuals played a significant rôle, while they were absent among bees sucking nectar.

Meager as the existing data are, they show a promising possibility for a systematic investigation of the selection and adaptation of the worker bees of different races to different plants. The preference of certain bee races for certain plants is the cause of differences in the quality of honey collected. It happens often that the color and flavor of the honey collected in the same locality by colonies belonging to different races differ greatly. This has naturally a certain importance from the point of view of the marketing of honey.

Another racial characteristic of commercial importance is the capping of the combs. Phillips (65) gives the following description of this phenomenon: "Some races of bees fill their honey combs more completely than others and when the honey is in contact with capping it gives the honey the appearance that is described as watery. When the capping is separated from the honey by an air space the capping appears white (or yellow, depending on the color of the wax). In general the black races seem to produce whiter comb capping than the yellow bees."

A long series of different characteristics of high economic importance has been attributed to different races. We cannot go into details of this part of the problem, especially because these characteristics have not yet been expressed in numerical form. According to the experience of American beekeepers "an important characteristic of Italians is the resistance to European foulbrood. In that respect they have been compared chiefly with German bees to which race they are vastly superior" (Phillips, 65, p. 211). The Caucasians are, so far as we know, the most gentle bees in the world.

Numerous observations have been published concerning the racial differences in productiveness. We believe that a scientific, statistically controlled contest, including the most important races, would be a very important enterprise for theoretical as well as practical conclusions.

TAXONOMICAL CONCLUSIONS AS BASED ON BIOMETRICAL DATA

In one of our papers (1) we expressed the opinion that the classification of the taxonomic categories below the rank of species ought to be made only on the basis of a detailed and thorough investigation of the geographical variation of a given species. An investigation of this kind, based on *Apis mellifera* L. as material, has been described in this paper. Our purpose now is to discuss the bearing of the results on taxonomy as well as on

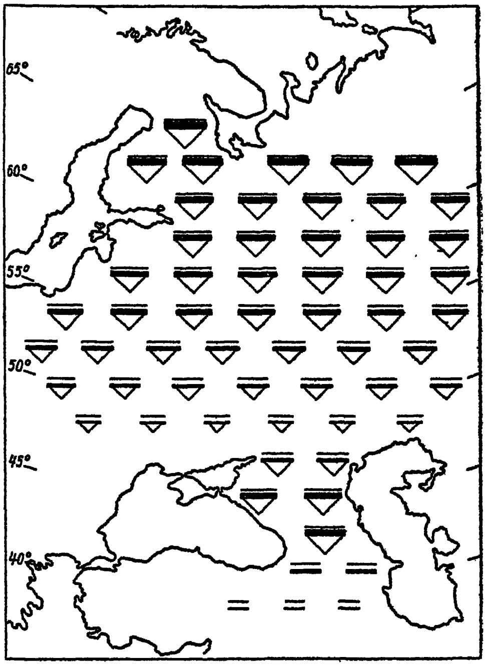

Fig. 19. Diagrammatic Map of European Russia

The size of each group of signs represents the size of the bees. The width of the middle bar corresponds to the coloration of the abdomen. The relative size of V-shaped sign represents the relative size of the wax gland surfaces. Owing to the lack of space North Caucasus is covered with signs corresponding to a more northern or mountain type of bee.

problems of variation in general. Our experience concerning the Russian plain and the Caucasus is generalized on the schematic maps represented in figures 19 and 20. The first map (Fig. 19) shows graphically the gradual change in body size, color, and relative size of the wax glands, while the absolute length of tongue and the relative length of the hind legs is shown on figure 20. As far as the Russian plain is concerned both maps show a harmonized change of characters from the north to the south. But when we start to consider Caucasus a pronounced difference appears between groups of characters represented on the two maps. The size of the body, coloration and relative size of the wax gland show, in the gray Caucasian mountain bee, a restoration of a picture existing in Middle Russia (i.e., far in the North), while the size of the tongue and the relative length of the hind legs show a continuous uninterrupted change southwards. Each of these two groups of measurements taken separately gives a splendid example of the gradual continuous geographical variation of two complexes of characters. It is perfectly clear that in the honey bees, at least in the area covered by our survey, the absolute size of the body (and of the wings), the relative size of the wax gland and the color of the abdomen are linked together and vary as a system. The same is true concerning the length of the tongue and the relative length of the hind legs. On the plain the two groups of characteristics are closely linked together but by a negative correlation. The situation is completely different in the Caucasus Mountains. Here the negative correlations disappear and we observe a complete independence in the variation of racial characteristics. Sumner (75) pointed out that the "existence of a correlation between two characters in the individual is not, in itself, sufficient to insure a constant correlation, geographically speaking." Our case brings evidence that the law of individual variation has a perfect analogy in group variation. Just as in the variations within the limit of a race we have correlative (negative and positive) variation, so the variation of group characters follows the same laws. It seems that we are justified in formulating two laws of geographical variation in the honey bee: (1) the variation is continuous and gradual, and (2) the characters of geographical forms may be correlated (positively and negatively) or may vary independently from each other. These two rules of the relationship of measurable

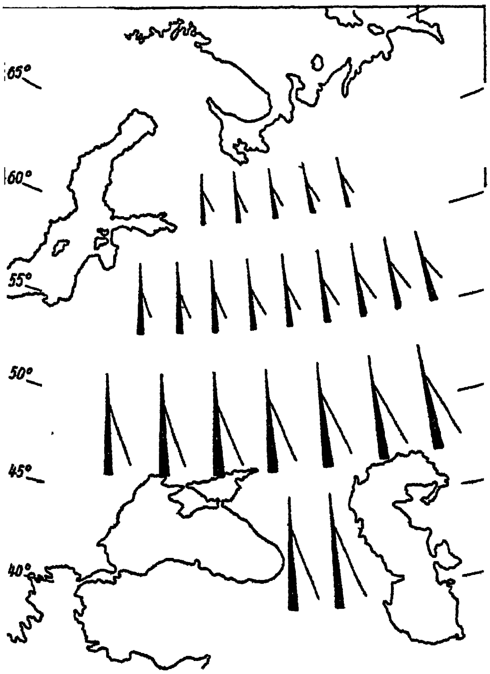

FIG. 20. DIAGRAMMATIC MAP OF EUROPEAN RUSSIA
The vertical bars with broader basis represent the tongue length. The lines attached to the right side of the bars show the proportion of legs to body size.

characteristics in the honey bee are very similar to the situation observed by Sumner in *Peromyscus* (75).

Before comparing in more detail the geographical variation of the honey bees with that of other animals we must connect our finding with the requirements of taxonomy. The first question concerns the reconciling of the usual methods of taxonomical description of lower taxonomical groups with the fact of the existence of a continuous geographical variation. One of the most definite determinations of a subspecies or geographical race was given by Semenov Tian-Schansky (73). It is as follows:

(1) Presence of one or several hereditary characteristics.
(2) Relative stability of these characteristics.
(3) Occurrence of intermediate forms linking two subspecific forms together in the area between the areas of distribution of the forms under consideration.
(4) A definite area of distribution.
(5) Psycho-physical isolation between the races being in the primitive stages of its development makes quite possible the production of a fertile progeny in inter-racial crosses.

Following this conception we feel justified in giving a special name to each local race of the honey bee inhabiting the plain of European Russia because each of them carries the peculiarities of a true geographical race. Increasing the number of points from which our material is taken we may increase unlimitedly the number of the races and each of them would require a special name. Sumner (74) has emphasized the importance of sections across the area of distribution "of a certain species by running a series of trapping stations through the territory of two adjacent subspecies at right angles to the supposed line of demarcation." He has also given two schemes of the interrelationships of subspecies which have a certain analogy with the scheme of Semenov Tian-Schansky (73) and our own proposed in the present paper.

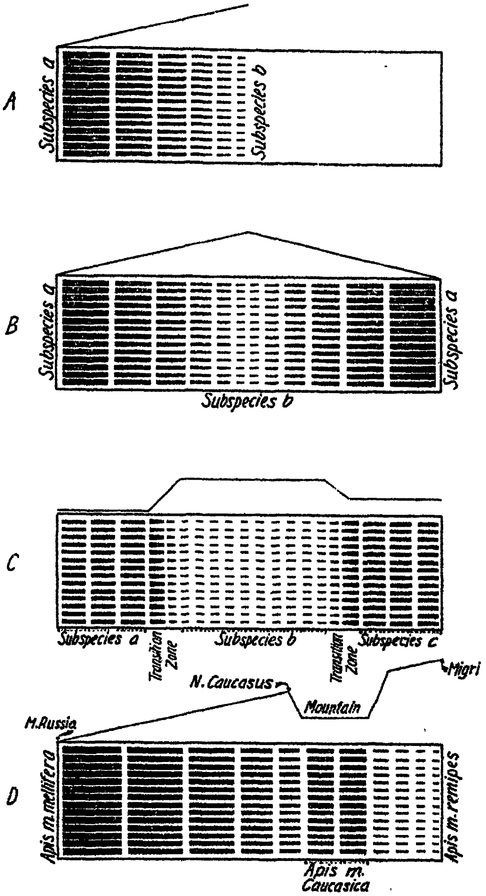

FIG. 21. DIAGRAMS REPRESENTING DIFFERENT TYPES OF GEOGRAPHICAL VARIATION

A. Gradual continuous variation.

B. Local form (*b*) surrounded by another (*a*) through a continuous chain of intergrades.

C. Local form (*b*), uniform in a certain area, connected with two others (*a* and *c*) by a comparatively narrow zone of intergrades.

D. Scheme of the north-south variation of the honey bee in Eastern Europe and Caucasus based on size of body, coloration and relative wax gland surface.

In figure 21 such a case is represented by diagram *A*. Some time ago in our papers on Russian Arctic Decapoda (1) we proposed to give subspecific names in cases of gradual geographical variation to extreme members of the geographical chain of forms. Examples of this first type of subspeciation are known to taxonomists of different groups. The variation of the honey bee on the plain of European Russia presents an example of just this kind if we do not consider the Caucasian bees as a continuation of the bees in European Russia.

A quite different case of a subspecies occupying a definite area in between the areas of another subspecies is represented in scheme *C* (Fig. 21). This is the most common type of geographical variation when the subspecific forms are connected with one another by a relatively narrow zone of transgressive forms. The subspecies of *Peromyscus* (Sumner) show this phenomenon in the clearest way. Besides that there may exist an intermediate type represented in the scheme *B*. In this case the subspecific names have to be given to the climax of the changes and to the extreme forms. We may apply the scheme just explained to the denomination of geographical forms of *Apis mellifera*. Four names must be considered: (1) *Apis mellifera* L., (2) *Apis mellifera caucasica* Gorbatschev, (3) *Apis mellifera ligustica* Spinola, and (4) *Apis mellifera remipes* Gerstäcker. There is no need to hesitate about the first and third of these names. They refer to the black European and Italian yellow varieties of the honey bee.

The taxonomy of the Caucasian bees has been far from clear. The west European taxonomists (Buttel-Reepen, Zander, 20, 83) identified all the Caucasian bees as *Apis mellifera remipes*, including in this conception yellow as well as gray Caucasian bees. A. N. Gorbatschev in 1916 recognized the independence of the gray mountain Caucasian bees from the yellow Caucasian bees, basing his conclusion on peculiarities of coloration, behavior, biology and specific area of distribution. He gave to the gray Caucasian bee the name *Apis mellifera caucasica* Gorbatschev. The origin of the name *Apis remipes* is as follows. This name is derived from a specimen of the honey bee belonging to the famous Russian zoologist Pallas, who recognized the specificity of Caucasian bees of the yellow type and described this form in one of his unpublished manuscripts. The specimen with the original label is preserved in the Berlin Zoological Museum and was mentioned in a few words by Gerstäcker (see Buttel-Reepen, 20). According to the rules of zoological nomenclature we have to consider Gerstäcker as the author of this form because Pallas never printed a single word concerning it. The question to solve is whether Pallas's description is of the gray mountain bee or of the yellow one. Koschevnikov (33) has expressed the opinion that the *Apis remipes* Pallas is identical with the Italian bees, in other words belongs to the yellow type. Gerstäcker in mentioning Pallas's specimen indicates that the bee was provided with yellow bands on the abdomen. The author of the present paper was able, thanks to the courtesy of the curator of the collection of Hymenoptera of the Berlin Zoological Museum, Prof. H. Bischoff, to reexamine Pallas's specimen, as well as his unpublished manuscript. Pallas gives in his manuscript the following indication about the origin of this Caucasian yellow bee: "Ad Caucasum lecta, itemque ex Hyrcania transmissa fuit." This means that Pallas obtained this bee near Caucasus and from the Southern coast of the Caspian Sea. It is evident that the Caucasian mountains were not the home of his species. Further on he writes: "Abdomen nudum, sessile, brevitur ovatum, testaceum basi, segmentis posteris nigro marginatis vel totis piceis, cano subfimbriatus, presertim subtus." It is clear that this description concerns a yellow bee. The small size and pronounced yellow coloration of the specimens preserved in the Berlin Museum permit us to conclude that the form described by Pallas and Gerstäcker under the name *Apis remipes* is certainly not the gray mountain bee.

We have already shown in an earlier part of this paper that the Italian bees are quite independent of the yellow Caucasian bees. This allows us to consider the yellow Caucasian bees as a form independent of *Apis mellifera ligustica* Spinola. Diagram *D* on figure 20 shows the scheme of relationship between *Apis mellifera mellifera*, *Apis mellifera caucasica*, and *Apis mellifera remipes*. There is a general trend of change from the north of Russia to Transcaucasia (Migri). *Apis mellifera mellifera* indicates the northern type of bees: *Apis mellifera remipes* is the expression of the southern type. But this trend is broken by the mountain chain populated by *Apis mellifera caucasica*, which is in most of its characteristics a reversion towards the northern type (except for the tongue length and the relative length of legs). The difference in tongue length between the Italian bees and the Caucasians gives certain indications that the rate of change in north-south direction in the East is more rapid than in the West. A very slight hint supporting this hypothesis is given by the fact that in Eastern parts of European Russia, on the same parallel of latitude, the bees seem to have a longer tongue than in localities situated farther west. It is very likely that the lines of identical racial characteristics of bees have the same south-western, north-eastern slope as do the summer months isotherms in Eastern Europe.

GEOGRAPHICAL VARIATION OF THE HONEY BEE IN RELATION TO THAT OF OTHER ANIMALS AND SOME PROBABLE EXPLANATIONS OF ITS SIGNIFICANCE

The purpose of the present section is to connect our findings on the variation of the honey bee with data derived from the study of other animals. As is clear from the previous discussion of the variation of different races of the honey bee, we consider this as one of the cases of geographical variation of a species along the area of its distribution. Looking around for material suitable for comparison we have to confess that such data are not very abundant. Although the insects have always been favorite objects for the discussion of the problem of variation we do not have any extensive work on the biometry of insects. Entomological magazines are full of descriptions of varieties, usually without any consideration of the importance of the biometrical method. It seems, therefore, that at the present moment variation of the honey bee is better known in a quantitative sense than that of any other insect.

Turning our attention to other groups of animals we do not find the situation to be consolatory, although examples of geographical variation are known to every taxonomist working in this or that particular group of animals. Series of analogous examples are brought together in some of the modern books like those of Hesse (31), Berg (19), and Robson (68), but unfortunately most of them do not have an exact quantitative treatment. Only a few groups of animals have been studied on the basis of exact measurements and statistical discussions of the numerical data. Looking for examples of such work we may refer to the investigations of Heincke (30) and J. Schmidt (71, 72) on fishes, Sumner (74, 75) on *Peromyscus*

(Rodentia) and Crampton (23) on Mollusca. The brilliant investigations of Schmidt and Sumner are particularly interesting, because of the application of experimental methods in the evaluation of the stability of subspecific (racial) characteristics. Our findings confirm perfectly the statements of these authors. Schmidt writes (71) "It is pointed out that the term 'races' of fish, as characterized by our population analysis, is only a statistical expression. The 'Race' is a mixture of different genotypes, where the proportions between these primarily, the environment only secondarily, exert determinative effects upon the average values which characterize the race." This is in accord with the phenomenon which we described above under the name of family variation.

As far as our experience goes the racial characteristics are strictly inherent. For instance, Schmidt says (72) that "the results of our transplantation experiments with *Zoarces* agree with the experiment with *Lebistes* previously described and confirm that the difference, proved to exist between the two populations, is of hereditary (genotypical) nature." All our experience with transportation of southern races of bees to northern localities in Europe and to the United States of America show the inheritance of racial characteristics. In that respect our data are in perfect agreement with Schmidt's (72) and Sumner's (75) findings on the stability of the subspecific (in other words racial) characters under changed conditions of the environment.

In regard to the origin of the differences of geographical forms, the general tendency of the investigators who have studied this phenomenon from the biometrical and experimental points of view is not to lay much stress on the influence of external conditions on the manifestations of geographical variation. Much more importance is attributed to the internal, i.e., hereditary factors. Crampton writes (23, p. 311) "In a word, the rôle of the environment is to set the limits to the habitable areas or to bring about the elimination of individuals whose qualities are otherwise determined—that is, by congenital factors," Schmidt (72, p. 10) concludes that

> the investigations and experiments with *Zoarces* described above have rendered new evidence of the correctness of the view, that the race characters in fishes are of a hereditary nature, i.e., that they are first and foremost determined by internal factors. That they are however on the other hand to a certain extent influenced by external factors, is here for the first time experimentally proved for one of our northern species of fishes. . . . . In view of the investigations hitherto undertaken the gradation of the average number of vertebrae has to be interpreted not as a direct effect of external conditions (the salinity or other factors acting parallel to it) but as a result of a selection.

Sumner (75, p. 254), discussing the problem of the origin of specific characters, expresses a very disappointing opinion "that we are not yet prepared to frame any adequate general hypothesis as to species formation."

H. F. Osborn in a recent paper (61) summarized in a brilliant form all of our knowledge relating to the problem of species splitting. He distinguishes distinctly the conception of mutation and speciation. The mutations arise suddenly. The process of speciation, on the other hand, indicates a phenomenon of differentiation of a species into subspecies connected with intergrading forms. Our material on bees must be listed in the category of phenomena of speciation. So far as the causes of this process are concerned Osborn leaves the reader without explanations.

The opinions of the leading authorities in this particular problem which have been quoted give evidence of the fact that at the present time we do not have any adequate explanation of the origin of geographical variation. A simple Lamarckian explanation, very popular among paleontologists and taxonomists, cannot be taken into serious consideration because of the lack of any credible experimental evidence of the inheritance of acquired characters.

We think it worth while, in looking for the explanation of the origin of geographical races, to turn our attention to the biological significance of the characters studied. In starting our work on the biometry of the honey bee—an insect of economic importance—we naturally did not fail to include in the investigation characters which have direct biological importance for the animal itself and hence for the beekeeper. Such characters are: the length of the tongue, size of the hind legs, size of the surface of the wax gland, and the size and number of hooks of the wings. It is very probable that all our biologically significant characteristics have a definite relation to the conditions of existence. The longer tongue of southern bees is probably connected with peculiarities of nectar secretion in the south as compared with the more northern localities. Michailov (39) suggested that the longer tongue of southern bees is an adaptation to dry conditions which lead to a lower level of nectar in the south, and thus compel the bee to have a longer working organ. We expressed (3) the hypothesis that the southern bees are obliged to have a longer tongue, not only because of a lower nectar level, but also because of a probable difference in the composition of the whole nectar secreting flora. It has been reported by many beekeepers that the southern, and particularly the Caucasian, bees can fly longer distances gathering nectar, and it is probable that their wings are in consequence more developed and have a larger number of hooks. The smaller size of the wax glands is probably connected with the condition that the bees in the South have perhaps less need to work upon the reinforcement of their nest. Hence the differences in the tongues, the wings and the wax glands (also probably in the first joint of the tarsus of the last pair of legs) may be considered as adaptations to different biological ends. It is probable that these characters have been developed by means of natural selection. Other characteristics like the general size of the body and coloration cannot at the present moment be even hypothetically evaluated as having any biological importance for the organism.

This discussion must stop here, unfortunately, because of the absence of comparable material on other insects. Aside from some indications as to the higher coloration and smaller body dimensions of southern insects we know little or nothing about this subject. It would be very desirable to develop active work in this direction. The large zoological museums furnish a tremendous number of opportunities for such investigations. It would be of great benefit to establish in large museums especially equipped biometrical laboratories, devoting their attention to geographical variation. The museums are real treasuries of material which, as a rule, has been worked upon only from routine taxonomical and zoogeographical points of view.

SUMMARY

1. This paper represents the results of five years of study on the biometry of the most important European races of the honey bee (*Apis mellifera* L.) being based on materials collected in their native locations as well as materials from the United States where the honey bee was

imported from Europe. The conclusions of this paper are based on the following material: (1) original measurements of more than 3000 specimens from 47 localities, (2) measurements of 10,000 specimens done in Russian Apicultural Experimental Stations and published mostly in previous papers by the author, (3) material (about 1500 specimens) published by A. S. Michailov and reproduced here in partly recalculated form.

2. One of the indispensable requirements in racial investigations on social insects is the consideration of differences which exist between colonies. The existence of family or colony variation is in this particular case demonstrated by the variation of number of hooks of bees belonging to different colonies. The variation of a colony represents only a certain part of the variation of the race. Hence it is advisable to take for racial investigation specimens from as many colonies as possible.

3. A. S. Michailov's data show that the following conditions of development have a pronounced effect on the body size of the worker bees: (1) the season of the development, (2) the temperature of the surroundings during the pupal stage, (3) the size of the cell, (4) feeding by nurse bees of different age, and (5) individuality of the colony. Recalculations of some data published by W. P. Michailov permit the addition to this list of the strength of the colony as a factor connected with the tongue length of the members of the colony.

Our original observations show that the size of the body is correlated with the reduction of the larval feeding period. In many cases the changes in absolute dimensions of the bee body have been accompanied by changes in proportions of the body. It is difficult to draw general conclusions concerning the character of the changes in proportions under the influence of different factors, each of them having a rather specific effect.

4. The geographical variation of bees is shown in the clearest form in the distribution of the average tongue length on the plain of European Russia. Bees even from neighboring localities differ in the average length of tongue, by showing a definite increase in length to the south. A linear equation is given connecting the latitude of the locality and the average tongue length.

5. Comparing bees from a northern locality (Middle Russia) with bees from the south (South Russia, North Caucasus and Italy) it can be seen that the southern bees are characterized by the smaller size of the body, larger number of hooks (North Caucasian bees being an exception), smaller relative surface of the first wax gland, relatively broader wings, and relatively longer legs. Our limited material on drones permits us to draw a conclusion about the smaller size of the drones in southern localities.

6. The black and yellow races of bees cultivated in the United States keep the same peculiarities which characterize the southern (yellow) and northern (black) races in Europe. They do not show any geographical variation analogous to that of Eastern Europe. On the other hand in regard to the variation of the tongue length the Americanized Italian yellow bee is not homogeneous, different apiaries being characterized by their own average tongue length. Being larger than Italian bees from queens born in Italy, American Italians are very close to the Ukrainian bees, differing from them, of course, in the coloration of the body and partially in the tongue length.

7. The bees inhabiting North Caucasus and Transcaucasia (Migri bees) represent a further step in the north-south scheme of

the variation in the honey bee. The mountain gray Caucasian bee is a reversion to the northern type, differing in many characteristics from the yellow Caucasian bees living in valleys.

A high relative length of the legs must be considered as a peculiarity of all Caucasian bees.

In respect to the length of the tongue the. Caucasian bees have the longest tongue among all races studied up to the present moment.

8. The transportation of bee races to new countries gives good material for judging the stability of racial characteristics. In that respect the bee races cultivated in the United States bring evidence that the racial differences between black and yellow races remain unchanged even in new habitats. Artificial selection (or perhaps the admixture of Cyprian blood) is the cause of the fact that the Italian bees cultivated in the United States are even lighter colored than the Italians from Italy. The size of the body of the American Italian bees seems to be larger than that of native Italian bees. There are evidences that the tongue length of bees inhabiting different parts of European Russia is also an inherent characteristic.

9. Parallel to the geographical variation in physical characteristics runs the variation of biology and behavior. Swarm instinct, number of extra queens, number of queen cells, preference in collecting the nectar from different plants, gentleness and capping of the combs are different in different races.

10. The geographical variation of the honey bee (*Apis mellifera*) has to be considered as one example of the geographical variation of animals in general. Two laws of geographical variation in the honey bee can be listed as follows: (1) the variation is continuous and gradual, and (2) the characters of geographical forms may be correlated (positively and negatively) or may vary independently from each other. In cases of gradual geographical variation it is proposed to use special names to designate the extreme links in the chain of geographical forms. Four new names are accepted to specify the geographical races of bees: *Apis mellifera mellifera* L. naming the North European black type of bees; *Apis mellifera ligustica* Spinola, the southwestern type of bees (Italian bees); *Apis mellifera remipes* Gerstäcker, south eastern type of Caucasian bees; and *Apis mellifera caucasica* Gorbatschev, the gray mountain Caucasian bee.

11. The geographical variation of the honey bee as compared with data on the geographical variation of other animals does not allow us at the present moment to draw any definite conclusions concerning its origin. Taking into consideration Osborn's distinction between mutation and speciation we have to list our material on the honey bee in the category of phenomena of speciation.

Some of the characteristics can be discussed from the point of view of their biological significance. Such characteristics are: the length of the tongue, size of the hind legs, size of the surface of the wax gland and the size of the wings and the number of hooks on them. It is probable that these characteristics have been developed by means of natural selection. Other characteristics like the general size of the body and coloration cannot at the present moment be considered even hypothetically as having any biological importance for the organism.

12. It is suggested, for the promotion of quantitative investigations in the field of geographical variation, to establish specially equipped biometrical laboratories in large zoological museums.

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EXPERIMENTAL STUDIES OF BIRD MALARIA

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INTRODUCTION

HUMAN malaria is undoubtedly the most important of all diseases in large areas of tropical and subtropical regions. It has been studied intensively by large numbers of first rate investigators during the past forty years, but there are still many problems to be solved, both scientific and applied. Some of these cannot be studied satisfactorily in man, although the recent discovery that general paralysis can be alleviated by malarial treatment has given an opportunity for controlled experiments with human beings from which results of importance have been derived. Fortunately birds are also infected with malarial parasites which resemble closely in their morphology and life-cycles the corresponding parasites of man. It is thus possible to use birds as experimental laboratory animals and to subject them to various conditions not possible in the case of human beings. Several very important discoveries in malaria have been made with the aid of birds. For example, MacCallum (1897) first observed in the blood of birds the process of gametogenesis and fertilization which had been troubling investigators for many years; Ross (1898) by his studies of bird malarial parasites proved that mosquitoes transmit malaria from one vertebrate host to another; and Roehl (1926) developed the valuable new therapeutic agent known as plasmochin as a result of experiments on birds.

During the past ten years, since the Johns Hopkins School of Hygiene and Public Health has been organized, canary birds infected with malarial parasites have been maintained in the laboratory of protozoology, and a number of investigators have carried out experimental studies with these organisms. In the following pages the writer has attempted to bring together some of the interesting results of these studies.

SPECIES OF BIRDS INFECTED IN NATURE

Malarial parasites belonging to the genus *Plasmodium* have been reported from many species of wild birds living in many countries; apparently they are especially common in birds of tropical and semitropical regions. According to Huff (1927) infections have been noted in at least 79 species of birds. These belong to at least 15 families included in the orders Anseres, Paludicolae, Columbae, Raptores, Pici, Passeres, and others. More species of the order Passeres have been found with infections than those of any other order, and members of the family Fringillidae appear to be particularly susceptible. The parasites now being used in the laboratories in the United States were obtained from English sparrows by Whitmore in New York in August 1913, by Hartman in Baltimore in October 1924, and by Huff in Hampton, Virginia, in September 1926.

GENERA AND SPECIES OF MALARIAL PARASITES IN BIRDS

Danilewsky (1885) was the first to report pigmented parasites in the red blood corpuscles of birds. Five years later, Grassi and Feletti (1890) gave to this organism the name *Haemamoeba praecox.* The genus name *Proteosoma* was later applied to it by Labbé (1894) and is still often used. Careful investigations have demonstrated, however, that the malarial parasites of man and birds belong to the same genus; hence the proper generic name of the latter is *Plasmodium.*

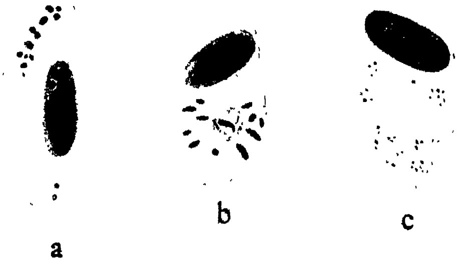

FIG. 1. GAMETOCYTES OF (A.) PLASMODIUM PRAECOX; (B.) P. CATHEMERIUM; AND (C.) P. INCONSTANS, SHOWING DISTINGUISHING CHARACTERISTICS

The dark oval body is the nucleus of the red cell. (After Hartman, 1927b.)

A genus of blood-inhabiting protozoa that is common in birds and resembles the genus *Plasmodium* in certain respects is *Haemoproteus* (*Halteridium*). A simple method of distinguishing one from the other is to observe the position of the nucleus of the infected red cell in relation to the parasite; in *Plasmodium* the nucleus is ordinarily pushed to one side by the invading organism; whereas in *Haemoproteus* the parasite grows around the nucleus without displacing it. Three kinds of malarial parasites in birds were reported by Celli and Sanfelice (1891) but were not described sufficiently to be recognizable. In practically all of the papers published up to the year 1927 the organisms studied were supposed to belong to a single species, usually called *Plasmodium praecox.* Hartman (1927b), however, believes that at least three species exist. For one of these, isolated from the Whitmore strain, he retains the name *P. praecox;* for the second, which is known as the Hartman strain, he proposes the name *P. cathemerium*, and for the third strain, obtained by Huff in Virginia, he proposes the name *P. inconstans.* Evidence has been secured by Manwell that the Whitmore strain may consist of two distinct varieties or species. The most important diagnostic characteristics of the three species as given by Hartman are as follows: *P. praecox* (fig. 1a) has elongated crescent-shaped gametocytes, schizonts that seldom occur in the peripheral blood, and an asexual cycle of about 24 hours (Hartman, 1927b); *P. cathemerium* (fig. 1b) has spherical gametocytes containing rather coarse, rod-shaped pigment granules, numerous schizonts in the peripheral blood, and an asexual cycle of 24 hours (Taliaferro, 1925; Hartman, 1927a); *P. inconstans* (fig. 1c) has nearly spherical gametocytes containing pigment granules that are approximately spherical and much smaller than those of *P. cathemerium.*

STAGES IN THE LIFE-CYCLE OF MALARIAL PARASITES

For the benefit of readers who are not familiar with the life-cycle of the malarial parasites the following brief account is presented (fig. 2). In nature the infective stage for the vertebrate host is a spindle-shaped body about 10 microns in length known as a sporozoite. Sporozoites are present in the salivary glands of infected mosquitoes and are injected into the

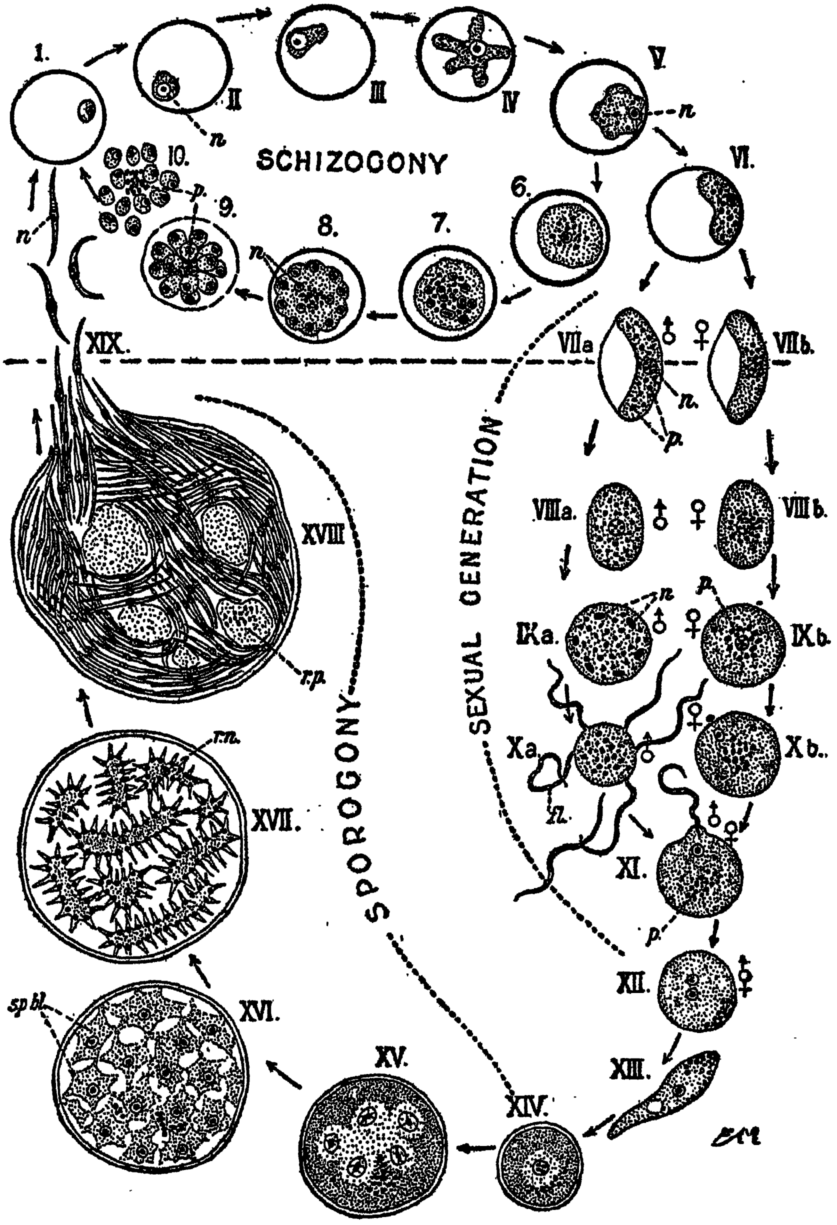

FIG. 2. DIAGRAM ILLUSTRATING THE LIFE-CYCLE OF PLASMODIUM FALCIPARUM IN MAN AND MOSQUITO

The stages shown above the line of dashes are passed through in the blood of man; those below the line, in the body of an anopheline mosquito. The asexual cycle (schizogony) begins with the sporozoite (XIX), which penetrates a red cell and becomes a trophozoite (I); this grows into a schizont (II–V), which segments into a number of merozoites (6–10), which in turn penetrate red cells and repeat the cycle. Some trophozoites develop into gametocytes (VI), which are of two kinds, microgametocytes (VIIa) and macrogametocytes (VIIb). The macrogametocyte breaks out of the red cell (VIIIb), becomes spherical (IXb), and throws off a polar body (Xb) thus becoming a mature macrogamete. The microgametocyte breaks out of the red cell (VIIIa), becomes spherical (IXa), and sends out 6 to 8 filamentous microgametes, one of which fuses with each macrogamete (XI), thus forming a zygote (XII). The zygote changes into an ookinete (XIII), which penetrates the stomach wall, where it rounds up into an oocyst (XIV). The oocyst grows large and within it arise hundreds of sporozoites (XV–XVII). These break out into the body cavity of the mosquito (XVIII–XIX) and some of them reach the salivary glands, where they are then ready to be inoculated into a new host. (From Hegner after Minchin.)

blood of the vertebrate host during the time these insects are biting. They penetrate red blood corpuscles, becoming amoeboid trophozoites, or schizonts, which derive their nutriment from the protoplasm of the red cell. By-products of the digestion of haemoglobin are deposited within the parasites in the form of dark brown pigment granules. When the trophozoite becomes fully grown its nucleus undergoes a number of successive divisions and it then breaks up into minute cells called merozoites. These merozoites escape from the corpuscles, penetrate fresh red cells and repeat the asexual cycle. Periodicity in malaria results from the simultaneous liberation of the merozoites. In benign tertian malaria of man the asexual cycle is 48 hours in length; in quartan malaria, 72 hours; and in estivo-autumnal malaria from 24 to 48 hours.

Certain of the parasites do not produce merozoites but become gametocytes; these are of two types, male or microgametocytes and female or macrogametocytes. The gametocytes are unable to complete their development while in the blood of the vertebrate host, and eventually die unless removed.

When a susceptible mosquito ingests blood containing gametocytes the latter are stimulated to further development in the insect's stomach. After undergoing a maturation process the macrogametocyte becomes a ripe macrogamete and the microgametocyte produces from six to eight whip-like processes which represent microgametes. Fertilization is accomplished by the fusion of one macrogamete with one microgamete, thus forming a zygote. The zygote elongates into a slug-like oökinete capable of locomotion. The stomach wall of the mosquito is penetrated by the oökinete, which becomes spherical and quiescent just beneath the outer epithelial layer. This oöcyst, as it is now known, grows at the expense of the surrounding tissue and within it develop large numbers of minute cells, the sporozoites, which eventually break out into the body cavity of the mosquito. Some of these sporozoites reach the salivary glands where they remain until they may be injected into a vertebrate host. The cycle in the mosquito requires from 8 to 20 days or more depending on the species of parasite and the temperature of the air.

THE RELATION OF THE PARASITE TO THE RED BLOOD CORPUSCLES

Laveran, who in 1880 first discovered the human malarial organism, believed it to be attached to the outside of the red cell. Most malarialogists, however, have since accepted the idea that the parasite is intracellular. Much discussion has been devoted to this problem, and a number of observations and experiments have recently been published which indicate that except in the sporozoite and merozoite stages the malarial organism is located within the red cell. Among those who oppose this view are Lawson (1913–1919), who reached the conclusion as the result of studies of stained slides that "All malarial parasites are extracellular, that is, they are attached to the external surface of the infected corpuscle and each parasite destroys several red corpuscles." Sinton (1922) supports this view as a result of subjecting infected human blood to hypertonic and hypotonic solutions; and De Langen (1925) comes to a similar conclusion because washing infected human blood cells in Ringer's solution brought about a reduction in the number of parasites in proportion to the number of red cells and apparently dislodged some of the fully grown parasites from the surface of the corpuscles. What appears to be the best method of determining the actual position of the parasites in relation to the red cells is that used by Ratcliffe (1927). Fresh blood from birds containing numerous specimens of *Plasmodium praecox*, and human blood infected with *P. vivax* was fixed in Bouin's fluid, sectioned 1.5μ or 2 μ thick and stained with Harris' haematoxylin. Material prepared in this way showed the parasites to be invariably inside of the wall of the red blood corpuscles and hence intracellular (fig. 3).

HOST-PARASITE RELATIONS IN BIRD MALARIA

The subject matter involved in the study of bird malaria may be indicated in terms of host-parasite relations. The writer has recently given an account of the biology of host-parasite relations of human protozoa in general (Hegner, 1926) and of intestinal protozoa in particular (Hegner, 1927). The relations between host and parasite include the following subjects: (1) The epidemiology of transmission, which deals with the infective stage of the parasite and its method of reaching and invading the host; (2) The distribution of the parasite within the host and the factors that lead to its localization in certain organs or tissues; (3) The natural or passive resistance of the host, by which is meant the obstacles that must be met by the parasite at the time of an invasion; (4) The natural or passive resistance of the parasite, which enables it to overcome these obstacles; (5) The character of the parasite's attack; (6) Changes in the host due to the parasitic invasion, such as symptoms, pathological lesions, and acquired resistance; (7) Changes in the parasite due to residence in the host, involving increases or decreases in resistance and aggressivity; (8) Host-parasite adjustments during an infection, which result in the carrier condition, latency and relapse; (9) Biological and chemical therapy; (10) Methods by which the progeny of the invading parasites reach the outside of the body; (11) Host-parasite specificity, including host susceptibility and parasite infectivity; (12) Methods of prevention and control, which may be considered personal hygiene in the case of the individual and public health measures when communities are involved.

MATERIAL AND METHODS OF RESEARCH

As already noted the laboratory strains of bird malaria that have been studied in this country have come from English sparrows captured in New York, Baltimore and Virginia. These strains all grow and reproduce when inoculated into canary birds. Female canaries have been employed almost exclusively as experimental animals because of the much higher cost of male birds. As Whitmore (1918) demonstrated, the blood of a bird once infected remains infective for a long time, in many cases probably as long as the bird lives. Whitmore found one bird to be infective 29 months after it was inoculated, and Mazza (1924) obtained

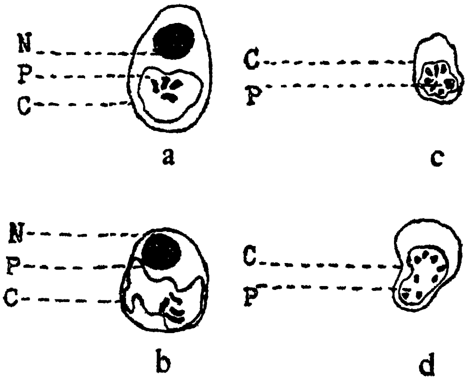

FIG. 3. MALARIAL PARASITES INSIDE OF RED BLOOD CORPUSCLES

Camera lucida drawings of sections of parasitized cells. *a*, *b*, *Plasmodium praecox* in red cells of bird. *c*, *d*, *P. vivax* in red cells of man. *C* = cell wall. *N* = nucleus of red cell. *P* = parasite. (After Ratcliffe.)

infections with the blood of a bird 4 years and 2 months after the original infection. During most of these periods parasites are so few in number in the peripheral blood that they cannot be found in films made according to the usual methods. Thick films of the blood of birds are of no value in the study of malaria since the red blood corpuscles of birds are nucleated and when clumped together obscure any parasites that might be present.

To transfer infection to a fresh bird the vein on the inner side of the leg of an infected bird is punctured with a Hagedorn needle just below the ankle joint and from 50 to 100 mg. of blood are drawn into a Luer syringe of the ¼ or ½ cc. size, containing a small amount of normal saline or citrated saline to prevent clotting. This mixture is then injected into the breast muscle, peritoneal cavity or the vein on the inner side of the leg. Intravenous injection is the most difficult method. It can best be done with a ¼ cc. Luer syringe fitted with a slightly bent #27 needle. The quantity of blood necessary to bring about an infection depends in part on the number of parasites in the infective blood and the natural resistance of the bird, but 100 mgs. of blood are practically always sufficient, unless the infective blood is obtained from a latent case, in which event 200 mgs. are often required.

Certain phases of the work require that gametocytes be distinguished from schizonts. The criteria for doing this, as worked out by L. G. Taliaferro (1925), are similar to those that have long been used in human malaria. The fully grown schizonts and gametocytes are about the same size and shape. The schizonts have mottled, medium-blue staining cytoplasm and pigment granules more or less clumped together. The macrogametocytes are characterized by darker-blue staining cytoplasm and dispersed pigment granules. In the microgametocytes the cytoplasm stains a very light blue and the nuclear material is often stellate in form.

A numerical expression of the degree of infection may be obtained in several ways. Ben-Harel (1923) obtained a ratio of parasites to corpuscles and the number of corpuscles present at a given time and from these data computed the number of parasites per cubic millimeter of blood. Frequent extraction of blood from a canary, which contains only about one cubic centimeter, interferes with the course of an infection; hence this method of counting has been discarded in favor of the following. A blood film is prepared and the ratio between the numbers of parasites and red cells is obtained by counting a number of microscopic fields. The proportion of parasites per 10,000 red cells is then calculated. If significant results are to be obtained one must know how large a sample must be examined, since this must be larger when a small number of parasites are present if a corresponding probable error is desired. A formula was worked out by Hartman (1927a) to determine how many corpuscles must be counted so that the probable error will be about 10 per cent of the observed number of parasites.

The desired probable error in equation form is: $PE_p = 1/10p$ in which PE_p is the probable error of the observed value and p is the observed value, i.e., the number of parasites per 10,000 red cells. The equation for the probable error is $PE = 0.67449\,\sigma$, in which σ is the standard deviation of the probability; and that for σ is $\sigma = \sqrt{\frac{p(1-p)}{N}}$, in which N is the number of units in the sample taken and p the observed frequency of the phenomenon under consideration. Substituting in the first equation above and solving for N we get $N = 45.494\,\frac{1-p}{p}$. This formula gives a means of calculating the size of sample (N number of corpuscles) which must be taken in order that the probable error of the relative frequency be one tenth of that frequency.

This formula is of value only if parasites are evenly distributed in a given sample. Tests indicate that the distribution of parasites in blood obtained as described above is uniform.

The periodicity of the asexual cycle in bird malaria necessitated a method of measuring the size of the schizonts. This was done by Taliaferro (1925) as follows. Parasites, 100 or 50 in number according to whether many or few were present, were drawn with a camera lucida, thus giving outlines of the organisms magnified 3000 diameters. The average length and breadth of these drawings were then obtained in micra, and their product divided by the number of parasites drawn. A modification of this method was used by Hartman (1927) who made camera lucida drawings and then computed their area in square microns with the aid of a planimeter.

Another method that was required to determine certain questions was that of obtaining the coefficient of variation. This was done by Taliaferro (1925) as follows:

1. The standard deviation was calculated by means of the formula.

$$\sqrt{\frac{\Sigma x^2}{n} - M^2},$$

in which x represents the magnitudes of the measurements (not their deviations), n the number of individuals and M the mean.

2. Finally, the coefficient of variation was derived by the formula.

$$\text{C.V.} = \frac{100\sigma}{M},$$

in which σ represents the standard deviation and M the mean.

DISTRIBUTION OF PARASITES WITHIN THE BIRD

Malarial parasites, when injected into a vertebrate host either in the sporozoite stage by mosquitoes or in the trophozoite stage by blood inoculation, are no doubt carried to all parts of the body in the blood stream. Malaria is often considered to be a disease of the peripheral blood, but the internal organs, especially the spleen, bone marrow, and liver, are liberally supplied with parasites. It has been suggested that the sudden decrease in numbers of parasites that occurs during the course of a normal infection might be the result of their segregation in certain tissues or organs. Ben-Harel (1923), Hartman (1927a), Dr. C. F. Scudder and Dr. R. F. Feemster (unpublished work) have all studied the tissues of the internal organs of birds at various stages of infections but have not found any evidence that migration from the blood into the tissues takes place. It seems certain therefore that the optimum habitat of bird malarial parasites is the blood stream and that the organisms are rather uniformly distributed throughout the body by the circulation of the blood.

An attempt was made by Boyd (1925) to determine the distribution of the parasites within the blood. He inoculated 10 birds with whole infected blood, 10 with washed red cells from infected blood and 10 with serum obtained by centrifuging whole infected blood and removing the serum with a pipette. No differences were found between the prepatent period and period of rise when whole blood and washed red cells were inoculated, but the prepatent period was over twice as long and only 4 of the 10 birds became infected when the serum was inoculated. This indicates that almost all of the parasites are within the red cells and very few in the serum.

PARASITOLOGICAL PERIODS

The parasitological periods differ for the three species of bird malarial parasites and vary in length in different canaries. Data derived by Boyd (1925) from 30 birds infected with the Whitmore strain give a prepatent period of from 1 to 11 days with an average of 5.33 days, a period of rise of from 2 to 10 days with an average of 5.33 days, and a period of fall of from 2 to 12 days with an average of 5 days. Parasite curves showing low, intermediate and high infections with this strain are presented in figure 4 (MacDougall, 1927). A number of factors other than the natural resistance of the bird may be responsible for modifications in the parasitological periods. Huff (1927), who had an opportunity to study the course of infections with the three species of parasites named by Hartman (1927b), records the prepatent periods as follows:

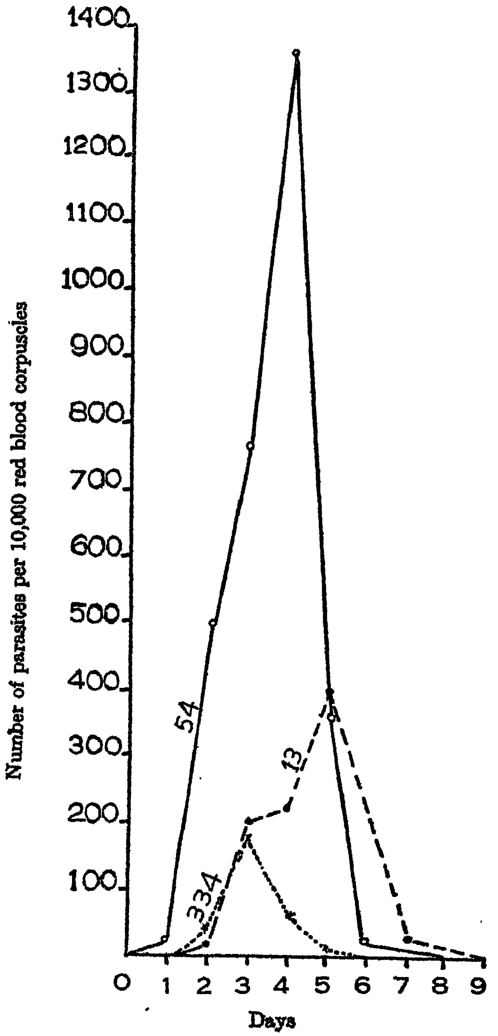

FIG. 4. CURVES REPRESENTING HIGH, INTERMEDIATE AND LOW INFECTIONS WITH BIRD MALARIA IN UNTREATED BIRDS

The data were obtained from birds 13, 54, and 334. (After MacDougall.)

PARASITE	NUMBER OF BIRDS	AVERAGE PREPATENT PERIOD
Plasmodium cathemerium......	39	5.78 ±0.14
Plasmodium praecox..........	18	11.44 ±0.45
Plasmodium inconstans.......	10	8.5 ±0.37

The average lengths of the prepatent period as here given indicate that this characteristic may be of taxonomic value.

The effects of variations in the number of parasites inoculated upon the length of the parasitological periods were tested by Boyd (1925). Five birds that were inoculated with 100 parasites each did not become infected; that they were susceptible was proved by the fact that they were all infected later with larger doses. It seems probable that many of the parasites that are injected into the breast muscle of a bird are destroyed by phagocytes or other agencies and that the 100 parasites used met this fate. Of 7 birds inoculated with 1000 parasites each, 2 became infected and 5 did not. Five of 6 birds inoculated with 10,000 parasites each were positive. The effects of the number of parasites inoculated upon the length of the prepatent period is indicated in the following table, the coefficient of correlation being −0.522 ±0.053.

NUMBER OF PARASITES USED FOR INOCULATIONS	LENGTH OF THE PREPATENT PERIOD IN DAYS												
	1	2	3	4	5	6	7	8	9	10	11	12	
1,000									1		1		2
10,000						1		1	1	1		1	5
100,000				1		1	2		3				7
200,000			2	1	8	1	2	2	1		1		18
1,000,000		2	4	3	6								15
5,000,000	1	4	4	3	2								14
10,000,000	4	3	4	3	3	1							18
20,000,000	1	2			1								4
	6	11	14	11	20	4	4	3	6	1	2	1	83

This table presents the prepatent period of 83 birds and proves conclusively that in general the length of this period depends directly upon the number of parasites inoculated, and that the greater the number of parasites the shorter the prepatent period becomes.

CLINICAL PERIODS

Symptoms of malaria, being largely subjective, have not been well determined for birds. Furthermore the temperature of birds changes so rapidly that thermometric readings are of little value. According to Hartman (1927a) one or more parasites to 100 red cells must be present before symptoms appear, although, as is to be expected, some birds with mild infections exhibit more severe symptoms than others with heavy infections. Symptoms, as in human malaria, occur soon after sporulation begins and continue for a shorter or longer period depending on the severity of the infection. The birds show signs of chills and fever, are more quiet than usual, and sit on their perches with their feathers ruffled up and often with the head under a wing. Weakness and loss of appetite may appear after the peak of the infection is passed.

NUMERICAL RELATIONS OF SCHIZONTS AND GAMETOCYTES

It is the general impression that the malarial sporozoites inoculated into the vertebrate host are of one type and all develop into schizonts. Some of them may develop into gametocytes but these would be very few in number and since they have no method of reproducing others of their kind would not account for the large number present in infections later in the course of the disease. According to Manwell the gametocytes of *Plasmodium cathemerium* can be found about 2 or 3 days after schizonts appear in birds infected by blood inoculation, and those of *P. praecox* at the end of the prepatent period, which is about 10 days in length. It seems certain that gametocytes as well as schizonts must develop from merozoites, even if some of them arise also from sporozoites. How this is brought about is problematical, but what we know of the cytological phenomena in the sex cells of higher organisms suggests that changes occur in the chromosome complex of certain schizonts such that all the merozoites produced by them develop into gametocytes or else similar changes take place during the segmentation of some of the schizonts, resulting in the formation of both schizont-producing and gametocyte-producing merozoites. What stimulates these hypothetical changes can hardly be conjectured.

Taliaferro (1925) found that during the acute period of an infection with *P. cathemerium* about 3 per cent of the parasites were gametocytes, and that during relapses and sometimes during the subpatent period the percentage of gametocytes ranged from 2 to 50. Huff (1927) made more detailed studies of the production of gametocytes during the course of infections with *P. cathemerium*. Figure 5 presents curves of an acute infection followed by a relapse induced by feeding sugar to the bird on the days indicated by asterisks. The prepatent period was in this case 9 days in length. During the succeeding 4 days the number of parasites per 10,000 red cells (heavy solid line) rose to a peak of 800 and then decreased until 4 days later. This was followed by a subpatent period of 3 days and by a relapse, which was more severe than usual. During the acute infection gametocytes were first noted on the tenth day, increased to 220 per 10,000 red cells during the succeeding 3 days (light solid line) and disappeared from the peripheral blood 2 days later. They reappeared at the beginning of the relapse on the twentieth day, increased to 260 per 10,000 red cells 3 days later and then decreased until they disappeared 5 days later. The percentage of gametocytes to the total number of parasites, as indicated by the broken line, increased continuously and rapidly during the acute infection from 4 per cent on the tenth day to 84 on the fifteenth day. The percentage of gametocytes remained comparatively low during the relapse (from 6 per cent to 13 per cent). Huff concludes that since symptoms appear at the time the peak of the infection is reached, at which time the percentage of gametocytes is nearing the maximum, and since mosquitoes have a better chance of biting a bird that is sick, therefore the increase in the number of gametocytes as indicated has a significant effect on the epidemiology of transmission, mosquitoes being more apt to become infected at just the time when the birds are most susceptible to their bites. He also concludes that since there is no periodicity in the production of gametocytes, day-biting and night-biting mosquitoes have an equal chance of transmitting the organisms provided both types of these insects are susceptible.

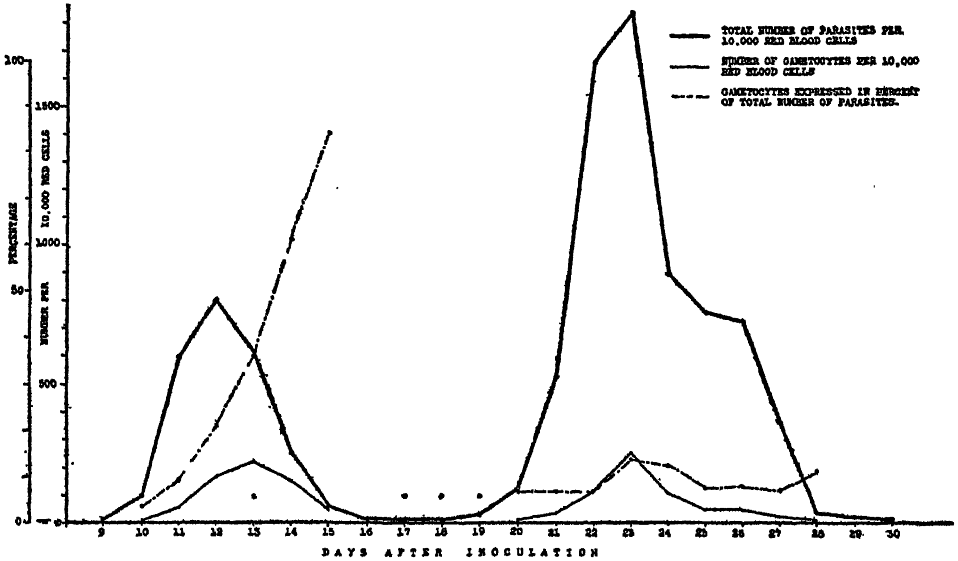

FIG. 5. COMPARATIVE NUMBERS OF GAMETOCYTES DURING AN ACUTE INFECTION OF BIRD MALARIA FOLLOWED BY A RELAPSE

The percentage of gametocytes (dots and dashes) increased throughout the acute infection but maintained almost a level during the relapse. Sugar was fed to this bird on the days indicated by asterisks. (After Huff.)

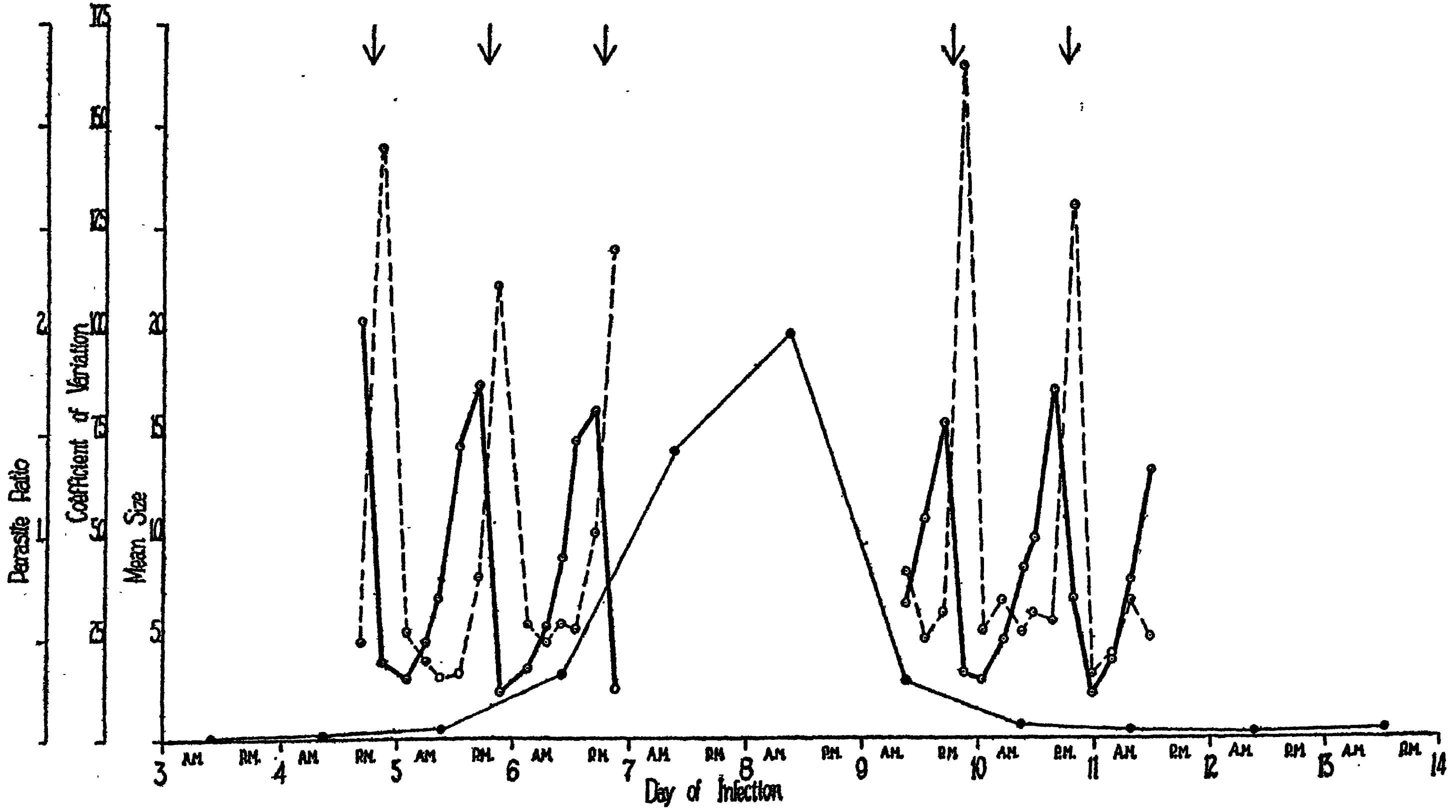

FIG. 6. MEAN SIZE (THICK LINE), COEFFICIENT OF VARIATION FOR SCHIZONTS (DASHES), AND NUMBER OF PARASITES PER 10 RED CELLS (THIN LINE) DURING AN INFECTION OF A BIRD WITH PLASMODIUM CATHEMERIUM

The distance between the peaks of the curve for mean size indicates the rate of reproduction, one generation per 24 hours; this rate of reproduction is no modified by the number of parasites destroyed. (After L. G. Taliaferro.)

PERIODICITY IN BIRD MALARIA

One of the principal characteristics of human malaria as a disease is the periodicity of symptoms. Soon after the true organism of malaria was discovered by Laveran it was found that symptoms appeared at the time the merozoites were liberated from the red cells. It was later definitely established that the asexual cycle of tertian malaria is 48 hours, of quartan malaria, 72 hours and of aestivo-autumnal malaria, 24 to 48 hours. Periodicity in bird malaria was demonstrated by Mrs. Taliaferro (1925) and confirmed by Drensky and Hegner (1926) and others. Mrs. Taliaferro found that there is a definite period for the asexual cycle in both the Whitmore and Hartman strains and that the synchronicity of reproduction is not affected by long passage from bird to bird. For example, measurements were made of 50 parasites from one bird at 4 hour intervals for several successive days and the mean size, coefficient of variation, and ratio of parasites to red cells computed. Figure 6 gives the results. The curve for mean size shows that the parasites were largest late in the afternoon; there were many large schizonts at this time, some in process of division. Within a few hours the mean size dropped abruptly to its lowest point; the parasites observed were mostly very small schizonts. Then a more gradual average increase in size occurred as the schizonts grew until at the end of 24 hours they reached their maximum size again. The curve of the coefficient of variation (fig. 6) shows that variability was greatest when the mean size was lowest; this is due to the fact that all of the schizonts do not produce merozoites exactly synchronously but a few lag behind so that both large schizonts and small trophozoites are present at the same time. The peaks of the curve in the figure indicate the length of the asexual cycle, which is 24 hours for the Hartman strain. It should be noted that the periodicity continues regardless of the relative number of parasites and also that periodicity is not modified by the large number of parasites that die during each asexual generation (see page 75). The fact that the rate of reproduction was found to be the same during the acute infection, the subpatent period, and subsequent relapses has a bearing on the subjects of resistance and relapse that will be considered more in detail later (see page 77).

ASEXUAL REPRODUCTION WITHOUT LOSS OF VITALITY

Free-living protozoa have been used extensively for the study of the question whether unicellular organisms are able to reproduce indefinitely without fertilization, but very little attention has been given to parasitic protozoa. The rate of asexual reproduction is usually accepted by protozoölogists as a measure of the vitality of a strain. Woodruff (1926) carried on a pedigree culture of *Paramoecium aurelia* derived from a single "wild" individual for 19 years, during which about 11,700 generations occurred without the intervention of fertilization (conjugation) and without loss of vitality, although an internal reorganization, named endomixis, was found to take place. That malarial organisms may likewise reproduce without the intervention of a fertilization process and without loss of vitality is indicated by our data (Hegner, 1926). Taliaferro (1925) found the asexual cycle of the Whitmore strain of bird malaria to be about 30 hours. This strain, as noted above, was obtained from an English sparrow in August 1913 and has been passed from bird to bird by blood inoculation ever since. This period consisted of about 131,400 hours. Dividing this number by 30 gives 4,380, which is approximately the number of asexual generations this strain passed through without the intervention of sexual reproduction.

If we accept twenty-four hours as the length of the asexual cycle in the Hartman strain the data are as follows: total period, about 4 years; number of days, about 1460; number of asexual generations, about 1460. Whitmore reported, in 1921, that three of his canaries remained infected with the Whitmore strain for 29 months (until their death) after they were inoculated—a period during which about 700 asexual generations must have taken place in a single host. Mazza (1924) records a bird that was still infective 4 years and 2 months after the original inoculation, but the number of asexual generations cannot be computed in this case because the length of the asexual cycle is unknown for his strain.

The length of the asexual cycle for the organisms of human malaria was noted above. It seems certain that asexual reproduction continues at the same rate throughout human infections as it does in those of birds, hence the number of asexual generations may be calculated approximately by dividing the number of days of the infection by the length of the asexual cycle of the species concerned. It is of course necessary to prove that the infection measured is due to one group of parasites and not to sporozoites inoculated by mosquitoes subsequent to the original infection.

Besides the rate of asexual reproduction another criterion of vitality exists among parasitic protozoa and that is virulence. The evidence shows that both the Whitmore and Hartman strains have maintained their virulence throughout the entire period since they were secured. A factor of interest in regard to the rate of reproduction and virulence observed is the constant environment in which the malarial organisms live.

Does reorganization take place during asexual reproduction in these organisms? This is a question that can not be answered. No such phenomenon is known, but this does not prove that a reorganization process is absent, since we know very few of the cytological details of the malarial parasites during reproduction. We do know that a differentiation takes place in the blood, resulting in the production of sexual cells from the asexual generation, but as stated above these sexual cells do not continue development in the blood. Perhaps other changes corresponding to endomixis occur at some stage during the growth of the schizonts or when the merozoites are formed.

GROWTH OF TROPHOZOITES

The synchronicity of the growth and reproduction of the malarial parasites is a truly remarkable phenomenon. It is not surprising that a group of sporozoites when inoculated into the blood of a vertebrate host by a mosquito should grow to full size and undergo schizogony at approximately the same time, but it is certainly astonishing to find this still going on after a strain has been maintained continuously in canaries by blood inoculation for 11 years (Taliaferro, 1925). The synchronous growth of the trophozoites of *P. cathemerium* is illustrated in figure 7, which shows, by means of camera lucida drawings, the sizes of the parasites at 4 hour intervals during one asexual generation. Some of the schizonts produce merozoites earlier than the others and some lag behind, but most of them segment at approximately the same time day after day. The variation in growth stages in the Whitmore strain, which was 11 years old, was found by Taliaferro (1925) to be only slightly greater than that of *P. cathemerium*, which had been passed through canaries for only a few months.

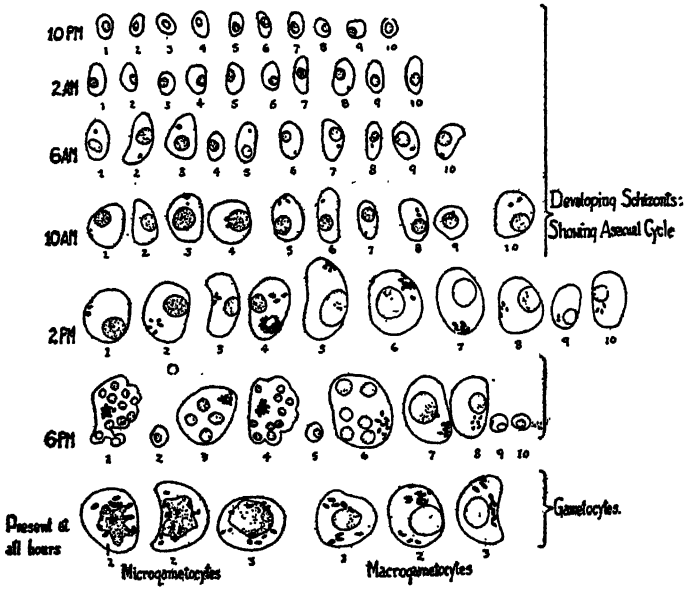

FIG. 7. REPRESENTATION OF THE CYCLE OF REPRODUCTION IN BIRD MALARIA SHOWING CHANGES IN SIZE AND VARIABILITY

Outlines of the asexual stages (× 1500) of the parasites (ten of each), showing nuclei and pigment granules, made at four-hour intervals during a consecutive period of 24 hours. In addition, outlines of three microgametocytes and three macrogametocytes, which occur in small numbers at all hours throughout the infection. The red cells in which the parasites were found have been omitted. (After L. G. Taliaferro.)

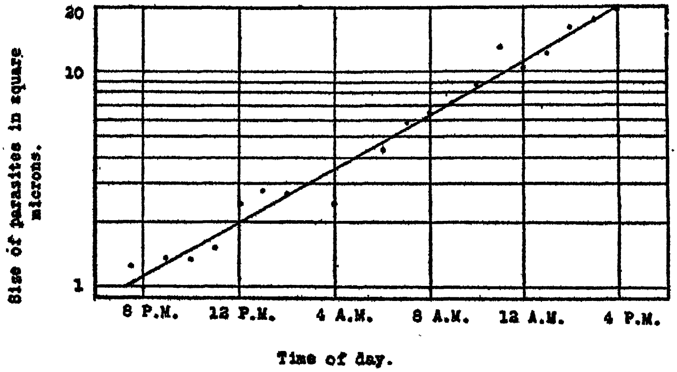

FIG. 8. GRAPH SHOWING THE GROWTH OF THE SCHIZONTS OF BIRD MALARIA (P. CATHEMERIUM), AS INDICATED BY MEASUREMENTS IN SQUARE MICRONS, DURING A 24-HOUR PERIOD (ASEXUAL GENERATION) (After Hartman)

The growth of the trophozoites of *P. cathemerium* was studied by Hartman (1927a). The average areas in square microns of 20 parasites taken from a bird at intervals of one hour for a period of 20 hours were obtained as described above. These measurements when plotted on semilogarithmic graph paper show that the rate of growth is constant throughout the asexual cycle (fig. 8). "It is possible that this growth period may fit that part of an autocatalytic growth curve which can be approximately fitted with an exponential curve." (Hartman, 1927a, p. 431).

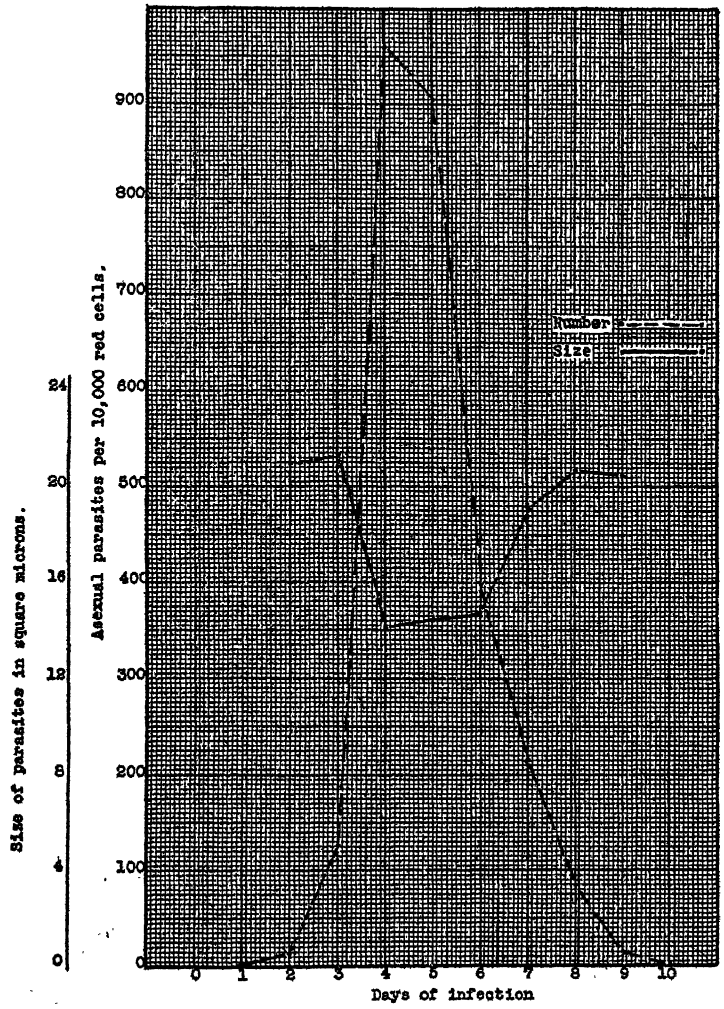

Fig. 9. Graph Showing the Decrease in Size of Bird Malarial Parasites as the Number per 10,000 Red Cells Increased and Subsequent Increase in Size as the Number per 10,000 Red Cells Decreased (After Hartman)

Studies by Hartman of the growth of trophozoites at different periods during the course of an acute infection with *P. cathemerium* have also brought out an interesting correlation between size and number of parasites per 10,000 red cells. Figure 9 presents the data for one bird. Average measurements were obtained as before from parasites taken at 3:00 P.M. on 8 successive days during an acute infection. The curves show a conspicuous decrease in size as the number of parasites increased to the peak and an increase in size again as the number of parasites decreased. Comparisons of the size of the trophozoites at the beginning of the infection and at the peak in at least 20 other cases confirmed these results. The factors responsible for this phenomenon are not known.

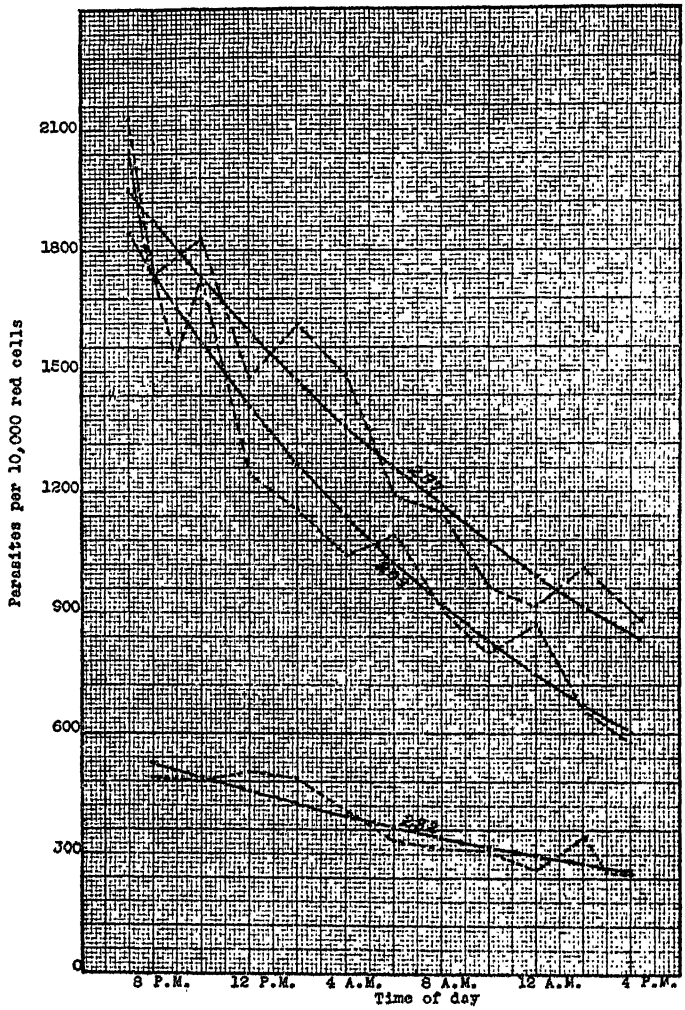

FIG. 10. GRAPH SHOWING THE DECREASE IN NUMBERS OF MALARIAL PARASITES PER 10,000 RED CELLS IN BIRDS 203, 282 AND 297 DURING A PERIOD OF 24 HOURS (ASEXUAL GENERATION)
(After Hartman)

MORTALITY DURING THE ASEXUAL CYCLE

The increase in the number of parasites during a single asexual generation and during the period of rise depends on various factors. In the first place different species of malarial parasites produce different numbers of merozoites at the end of each asexual cycle. Thus of the human tertian parasite, *P. vivax*, a single schizont may give rise to from 15 to 24, of the quartan parasite, *P. malariae*, to from 6 to 12, and of the estivoautumnal parasite, *P. falciparum*, to 8 to 10 or more. In the Hartman strain of bird malaria, *P. cathemerium*, the number of merozoites per schizont, according to Taliaferro (1925), ranges from 10 to 20 with 16 as the mode and 15.5 ± 0.11 the mean. If all of the merozoites produced were to succeed in penetrating fresh red cells, in developing into schizonts and in reproducing, the number of parasites present at the end of each asexual generation would be on the average 15.5 times that of the preceding generation. A certain percentage must be deducted from the mean number 15.5 to account for those merozoites that develop into gametocytes, a number estimated by Taliaferro as 3 per cent, thus bringing the mean down to 15.03. Counts, however, prove that no such increase occurs, but that in each succeeding asexual generation there are from 5.05 to 8.96 times as many parasites as in the preceding generation. These data indicate, therefore, that from 6.07 to 9.98 of the 15.03 merozoites perish in each asexual generation during the period of rise of an acute infection.

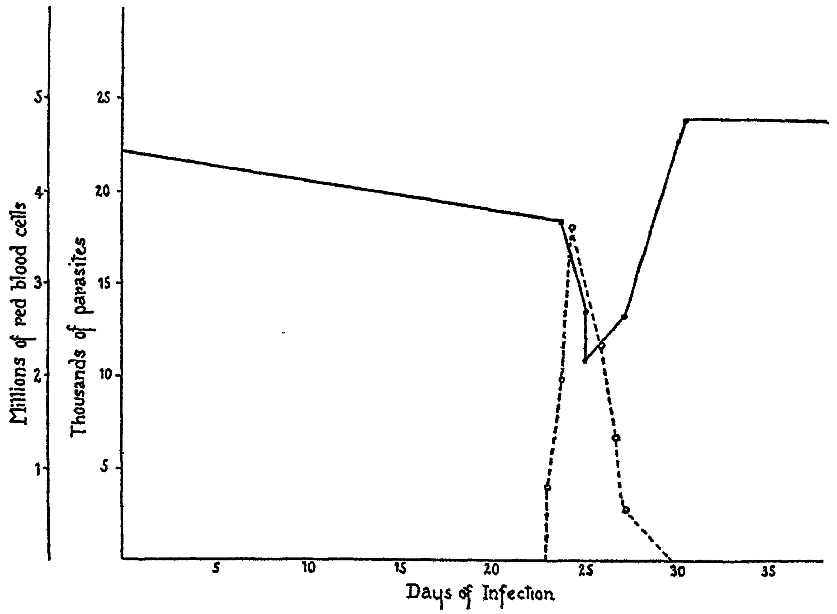

FIG. 11. CURVES SHOWING A DECREASE IN THE NUMBER OF RED CELLS (SOLID LINE) DURING THE PREPATENT PERIOD (1ST TO 23RD DAY) AND ACUTE PERIOD (23RD TO 25TH DAY) AND SUBSEQUENT INCREASE ABOVE NORMAL (After Ben-Harel)

This enormous mortality of parasites is most easily accounted for by assuming that many of the newly liberated merozoites are phagocytized, or killed by the blood serum, or fail to penetrate fresh red cells, but Hartman (1927a), by making counts at intervals of one or two hours during the asexual cycle, showed that the mortality is constant throughout the period. The results obtained from infections in 3 canaries are plotted in figure 10 with the solid lines representing the computed numbers and the dotted lines the observed numbers of parasites at intervals of one or two hours. It is obvious that there is a constant mortality rate during a single asexual cycle and not simply a mass destruction at the time merozoites are formed. This mortality rate is a mathematical constant, since the data fit approximately an exponential curve.

Apparently then parasites of all ages perish during the asexual cycle, not only merozoites before they penetrate the red cells but also young trophozoites and older schizonts. The natural death of red cells and the disintegration of red cells due to the penetration of the parasites may account for at least a part of this destruction. On the other hand other problematical factors may be in operation since, as Hartman points out, the increases and decreases in the numbers of parasites resemble mathematically the rise and fall of a population of free-living animals.

EFFECTS OF MALARIA ON THE BLOOD

One of the most striking characteristics of malaria is anemia due to a decrease in the number of red blood corpuscles. Even during the prepatent period, as Ben-Harel (1923) has shown, the number of red cells falls off, and during the acute infection the loss is very great (fig. 11). As the number of parasites decreases after the peak of the infection the red cells increase in number, and, at least in some cases, become more numerous than before the infection. Destruction of red cells is obviously brought about at the time of schizogony when the merozoites are liberated, but calculations show this to be insufficient to account for the number destroyed. Parasitized red cells may also disintegrate during the growth of the schizonts but to what extent is unknown. It has been suggested that toxins produced by the parasites are capable of hemolyzing red cells that are not parasitized (Celli, Carducci and Casagrandi, 1902, 1903). Boyd (1925) tested this idea by subjecting normal red cells to the action of serum from infected birds at a temperature normal to the canary, but without any evidence of hemolysis. Phagocytosis has also been suggested but little supporting data are available.

That there is an attempt within the bird to replace the red cells that are destroyed is indicated by the increased activity of the blood-forming organs during the infection and the increased number of young red cells that appear in the circulation. During the subpatent period the blood regains the normal number of red cells and continues in this condition unless disturbed again by a relapse.

EFFECTS OF MALARIA ON THE SPLEEN

Another conspicuous characteristic of malaria is the enlargement of the spleen. This occurs both in human malaria and in bird malaria. In normal birds the spleen measures approximately 3 mm. by 2 mm., and is bright red in color. In parasitized birds the spleen begins to enlarge soon after parasites appear in the blood and may reach a size of 15 mm. by 5 mm. (Ben-Harel, 1923). It becomes almost black and quite hard. The spleen usually becomes smaller as the infection lessens in severity but does not quickly regain its normal size and color. Within the enlarged spleen are present two types of pigment, dark brown pigment, which is a by-product of the digestion of hemoglobin by the parasite, and light brown pigment, which comes from the hemoglobin that is liberated when the red cells break down. The lumina of the splenic capillaries contain large numbers of parasitized red cells, and also phagocytized parasites and the debris of destroyed red cells. Other characteristics of the spleen of parasitized birds are the destruction of endothelial cells, an increase in the number of large mononuclear cells, and the presence of young parasites either free or attached to mononuclear cells. The asexual reproduction of malarial parasites was observed by Ben-Harel (1923) in the spleens of birds that were examined from 2 weeks to 6 months after the end of the acute infection.

RESISTANCE OF THE HOST

The term resistance is used here for any condition in the parasite's environment within the host that is detrimental to the parasite. This resistance, as noted above, may be either natural or acquired, natural resistance referring to adverse conditions present at the time of the original invasion and acquired resistance to adverse conditions built up by the host during the course of the infection. Since the length of the asexual cycle of the bird malarial organisms is known and is constant, and also the average number of merozoites produced by each schizont, it is possible to use the numbers of parasites present at any time during a carefully followed infection as a measure of the resistance developed by the host.

If all of the parasites produced by asexual reproduction were to live and in turn reproduce, the number of parasites present in a host would increase on the average about 15 times every 24 hours (in *P. cathemerium* in which the asexual cycle is one day in length). This would continue until so many of the red cells had been parasitized that the death of the bird would occur. During the course of the infection, however, over one-half of the parasites perish during each asexual cycle and enormous numbers are destroyed at and following the peak of the infection. This destruction continues until no more parasites are to be found by ordinary routine methods in the peripheral blood and continues during the subpatent (latent) periods and during periods of relapse, since it has been shown that reproduction continues at the same rate during the entire course of the infection. The constant mortality of parasites during the asexual generations is probably due to the natural resistance of the host, such as phagocytosis, toxicity of the blood serum, death of parasitized red cells, and resistance of the red cells to the penetration of merozoites. The greater mortality of parasites at and after the peak is probably due, on the other hand, to resistance acquired by the host. The immunological basis for this resistance is unknown. During the subpatent (latent) periods the bird is in the carrier condition, that is, it is infected but does not exhibit symptoms. At this time parasites are being produced at the same rate as during the acute infections but most of them are destroyed in each asexual cycle. If a decrease in the resistance of the host occurs the parasites are enabled to increase rapidly in number and thus bring about a relapse. Relapses, as will be described later, may be brought about experimentally and hence the resistance of the host can be modified by known factors.

VIRULENCE OF THE PARASITE

Changes in virulence during the course of infections and of epidemics have been recorded for many pathogenic microörganisms. Boyd (1925) attempted to determine whether such changes occur in bird malarial parasites. The first experiments were designed to test virulence during the acute infection. Fifty birds were divided into 4 groups. The first were inoculated with parasites obtained from birds during the first and second days after their appearance in the blood; the second group with parasites taken on the third and fourth days; the third group with parasites taken on the fifth and sixth days; and the fourth group with parasites taken at various times during the subpatent period.

Although these data show that the average length of the prepatent period and period of rise are shortest when parasites taken from birds during the third and fourth days of an acute infection are inoculated and that they are therefore most virulent at this time, the differences are not great and may be due to differences in the number of parasites inoculated or to individual differences in the resistance of the birds inoculated. The results may be tabulated as follows:

GROUP	PREPATENT PERIOD IN DAYS		PERIOD OF RISE IN DAYS	AVERAGE NUMBER OF PARASITES PER 10,000 RED CELLS AT PEAK
	Range	Average		
1	2–11	5.8	5.3	911
2	3–11	5.1	4.3	560
3	3–8	5.4	4.9	769
4	4–10	7.25	5.8	409

An attempt was also made by Boyd to increase the virulence of the parasites by rapid passage from bird to bird. Twenty-four birds were used. Each was inoculated with parasites from the preceding bird taken on the third day of the acute infection. The data obtained show no significant change in virulence that can be attributed to the rapid passage from bird to bird.

EFFECTS OF THE SUGAR CONTENT OF THE BLOOD ON THE COURSE OF THE INFECTION

Malarial parasites while in the body of the vertebrate host live in the blood stream, which constitutes a very constant environment. However, changes in the blood stream, advantageous or detrimental to the parasite, seem to take place since there are increases and decreases in the number of parasites at different stages of the infection. That the sugar content of the blood might be an important factor in the parasites' environment was suggested to the writer by the fact that Bass and Johns (1912) were unable to cultivate human malarial organisms in artificial media without the addition of sugar, and that they (1913) seem to have succeeded in cultivating these parasites in the blood of a diabetic without the addition of sugar. The fact that certain provocative agents, such as epinephrin, are known to bring about an increase in the sugar content of the blood is also suggestive. For these reasons Hegner and MacDougall (1926) and MacDougall (1927) studied the effects of changes in the sugar content of the blood on the course of infections in canaries with bird malaria. To increase the sugar content of the blood, one gram of glucose was dissolved in one cc. of water and one tenth of this was fed to each bird 4 times per day, at 3, 5, 7 and 9 P.M., a period during which schizogony occurs in the species of parasite studied, *Plasmodium cathemerium*. To decrease the sugar content of the blood 2 units of insulin were injected intraperitoneally daily. The results of the experiments indicate that the sugar content of the blood is an important factor in the environment of the parasite. In figure 4 are presented normal parasite curves of high, intermediate and low infections. In figure 12 are presented parasite curves from four birds that were fed sugar throughout the course of the infection. In bird 328 the number of parasites steadily increased until death occurred on the eleventh day, when 2,430 parasites per 10,000 red cells were present. The number of parasites remained high in bird 329 for several weeks, then decreased for a few days and then rose again, at which point the bird died. Bird 370 suffered three relapses in quick succession and finally died. In contrast to these are the parasite curves shown in figure 13 obtained from birds into which insulin was injected throughout the course of the infection. These curves represent all low infections and none of the birds died. From the experiments on these and many other birds it was concluded that increasing the sugar content of the blood by feeding sugar to infected birds is favorable for the parasite, whereas decreasing the sugar content of the blood by injecting insulin into the bird is unfavorable for the parasite.

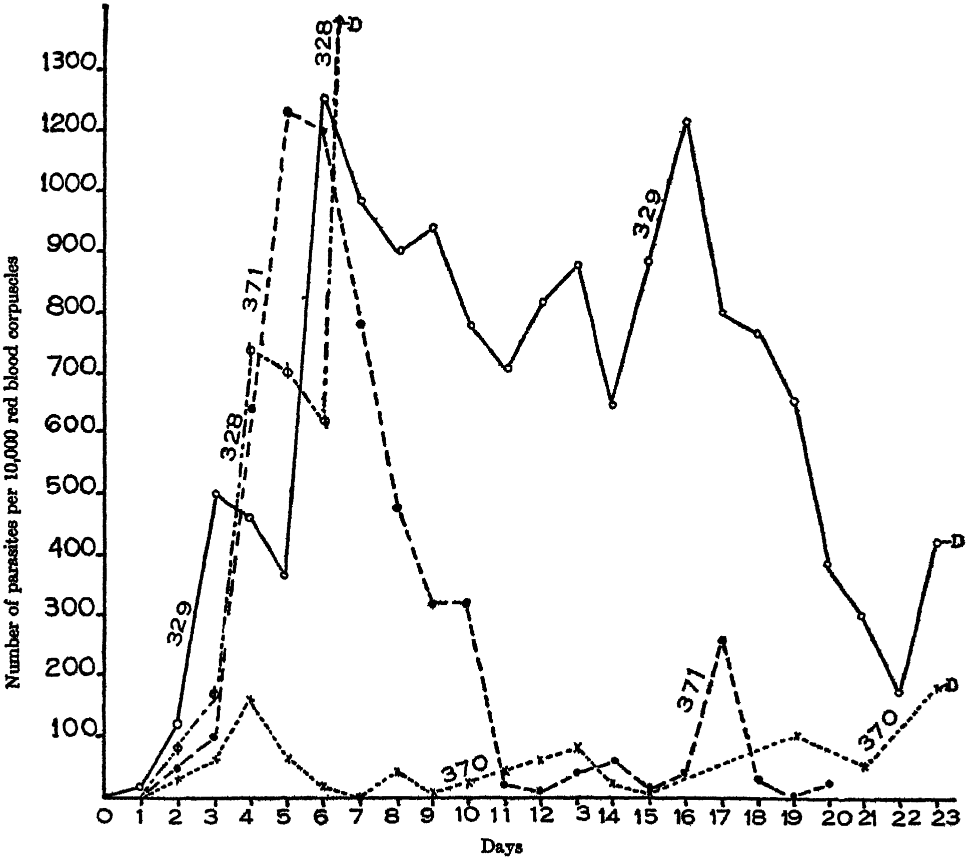

FIG. 11. CURVES SHOWING THE COURSE OF TYPICAL INFECTIONS WHEN SUGAR IS FED TO BIRDS DAILY

D signifies the death of the bird. *D** = death occurred on the eleventh day, when 1,430 parasites per 10,000 red cells were present. (After MacDougall.)

RELAPSE IN BIRD MALARIA

"Recovery" from an attack of malaria is usually the result of a decrease of parasites to a number insufficient to bring about symptoms; this decrease may be due to resistance acquired by the host or to treatment with quinine or some other drug. In probably most cases all of the parasites are not destroyed; a low grade infection continues until a change in the resistance of the host enables the parasites to increase to such an extent as to bring about a renewal of symptoms, a condition known as a relapse. Clinical relapses occur in about 65 per cent of infections with quartan malaria, 55 per cent with tertian malaria and 45 per cent with estivoautumnal malaria. Parasitological relapses may occur independently of clinical relapses, that is, an increase in the number of parasites may take place, as indicated by blood examination, but not great enough to induce symptoms. In certain respects relapse is the most important of all problems in malariology. For example, in some localities malarial organisms are not carried through the winter in mosquitoes but exist only in human hosts in small numbers. With the advent of spring relapses occur, often at the time when mosquitoes become active. From these relapsing cases the mosquitoes become infected and transmit the disease to others. Thus man serves as a reservoir which becomes effective when relapses appear. If all of the parasites within the human host could be destroyed, or if relapses could be prevented, malaria could be practically annihilated in many localities.

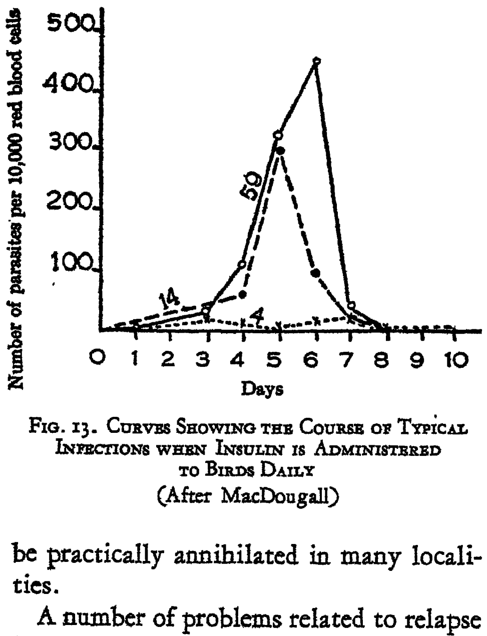

FIG. 13. CURVES SHOWING THE COURSE OF TYPICAL INFECTIONS WHEN INSULIN IS ADMINISTERED TO BIRDS DAILY
(After MacDougall)

A number of problems related to relapse have been studied by Manwell (1929), who kept accurate data of parasitological relapses for a large number of birds infected with all four of the strains maintained in this laboratory, and who also carried on certain interesting experiments. It was found that a seasonal variation in the relapse rate occurs in birds as it does in man. The greatest number of relapses were noted in the fall and winter and the smallest number in the summer. The four strains differed in their liability to relapse just as do the three species in man; the Whitmore strain relapsed in 61 per cent of the cases, *Plasmodium praecox* in 36.5 per cent, *P. inconstans* in 25.8 per cent, and *P. cathemerium* in 5.5 per cent. The susceptibility of individual birds to relapse varied; for example, 60 per cent of the birds infected with *P. cathemerium* did not relapse and most of the relapses recorded for this species occurred in 20 per cent of the birds. Some birds relapsed as many as 8 or 10 times, the result being great emaciation often followed by death. Relapses were most frequent immediately after the acute infection and least likely 3 months after inoculation; then the rate increased gradually for the rest of the year. The relapses in birds were light when compared with those of man but seemed to have a greater effect on the health of the bird. It may be that malaria resulting from blood inoculation does not induce relapse as frequently as that set up by sporozoites inoculated by mosquitoes; this appears to be true in human malaria (York, 1925). In some cases severe infections were not followed by relapses, whereas birds with mild infections had many relapses. *P. cathemerium*, for example, brought about the severest infections but the fewest relapses, resembling in this respect infections in man with *P. falciparum.*

The part played by environmental factors in bringing about relapse is problematical. Relapses in human malaria are often attributed to sudden changes in temperature, altitude, sunlight, etc., but canaries can be maintained under fairly constant conditions. High temperature and high humidity combined seemed to be a factor in the relapses recorded by Manwell, but exposure to direct sunlight had no apparent effect.

Those who believe that the human malarial parasites all belong to one species find support in the fact that sometimes an individual will undergo a tertian relapse in the spring followed by an estivo-autumnal relapse in the fall. This is presented as evidence that the tertian parasites transform into estivoautumnal parasites, both being different stages of one species of organism. Data obtained from the study of bird malaria support the view that the three species named by Hartman, as well as the Whitmore strain, are distinct species and not different manifestations of one species. Manwell has found that in infections with any one of these four strains the parasites retain their characteristics throughout the relapse period as well as the acute period.

BIRD MALARIAL PARASITES IN MOSQUITOES

Human malaria is transmitted by certain species of mosquitoes belonging to the genus *Anopheles;* mosquitoes belonging to other genera are all non-susceptible. On the other hand no species of the genus *Anopheles* are capable of transmitting bird malaria. Very little work has been done in recent years on the susceptibility of mosquitoes to bird malarial parasites. Huff (1927) lists three species of *Culex*, three of *Aedes* and one of *Theobaldia* that were known to be susceptible up to the year 1927. To this number Huff adds two more species of *Culex* and confirms previous positive results with two species of *Culex* and one of *Aedes*. He obtained negative results with five species of *Aedes*, one species of *Psorophora* and one species of *Anopheles*. In most cases suceptible mosquitoes became infected by all three species of bird malaria parasites.

The work of Huff on the fate of malarial organisms within the stomach of various species of mosquitoes has an important bearing on the problem of susceptibility and resistance to infection by these insects. The general impression among malariologists is that in susceptible mosquitoes asexual stages are killed and digested but gametocytes are stimulated to continue their development, whereas in non-susceptible mosquitoes both asexual stages and gametocytes are killed and digested. Huff, however, finds that although asexual stages are killed and digested in about 5 or 6 hours in both types of mosquitoes the gametocytes are stimulated, also in both susceptible and non-susceptible mosquitoes, to undergo maturation, fertilization and the formation of oökinetes. For example, oökinetes first appeared at the end of 12 hours in both *Culex pipiens*, a susceptible species, and *Aedes sollicitans*, a non-susceptible species, remaining in the former for at least 39 hours and in the latter for at least 20 hours, but they appeared to be unable to penetrate the stomach wall of *Aedes sollicitans* and hence could not continue their development into oöcysts. Susceptibility to infection is therefore not the result of differences in digestion but is due to some unknown reaction between oökinetes and the tissues of the stomach wall.

That differences in susceptibility exist among the individuals of a single species of mosquito has also been demonstrated by Huff. For example, one group of *Culex pipiens* mosquitoes were fed on a bird containing 1,213 parasites per 10,000 red blood cells, of which 37 per cent were gametocytes. Although every one of these mosquitoes must have ingested from 80,000 to 100,000 gametocytes only 7 of a total number of 15 that were dissected were found to have become infected. Apparently this result was due to differences in the individual mosquitoes; those that did not become infected possessed individual immunity. The basis for this immunity is unknown.

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MENDELIAN INHERITANCE IN FISH

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FISH have until recently received scant attention from geneticists. Yet the relatively few studies thus far made show that they offer favorable material for such work and are likely to prove especially useful in problems of the relation between the genes and the processes of development. Fish often show brilliant color patterns that are easy to follow in inheritance or in embryonic development. Certain aquarium fish attain sexual maturity in periods less than a year, making them comparable with the rodents in rapidity of breeding.

There are, however, two principal limitations of fish for these purposes, the difficulties of cytological studies of their chromosomes and the high mortality of young fish, which is likely to prevent careful studies of strength of linkage and frequency of cross-overs.

Various independent lines of investigation are converging to give information bearing on genetic work with fish. First there have been the observations of field naturalists and systematists, who have shown that certain groups of fish appear to be far more variable than others; secondly those of the aquarists, especially the German aquarists, who through the medium of their principal Journals, the *Blätter für Aquarien und Terrarienkunde* and the *Wochenschrift für Aquarien und Terrarienkunde* have accumulated information in regard to the characteristics, care and possibilities of scientific investigation of aquarium fish. The scientific work in government and commercial fish hatcheries has also been an aid, and finally the professional zoologists and geneticists are beginning to utilize fish in their investigations.

The writer wishes to make acknowledgment of the usefulness of Bashford Dean's *Bibliography of Fishes* as a guide to the earlier literature and to the kindness of Dr. E. W. Gudger, who has made fully available the continuation of this Bibliography, which is maintained in card catalog form at the American Museum of Natural History, New York City.

CLASSIFICATION OF FISH UTILIZED IN GENETIC INVESTIGATIONS

The following outline classification (based on Jordan, 1923) indicates the position of the various genera of fish that have thus far been utilized in genetic investigations and that are reviewed in this paper.

- Super Order Teleostei
  - Order Eventognathi
    - Family 237 Cyprinidae
      - Genus *Carassius*
        - Species *C. auratus*
  - Order Cyprinodontes
    - Family 290 Cyprinodontidae (Killifishes)
      - Genus *Oryzias*
        - Species *O. latipes*
      - Genus *Lebistes*
        - Species *L. reticulatus*
      - Genus *Rivulus*
        - Species *R. urophtalmus*

Family 294 Poeciliidae
(Top minnows)
Genus *Platypoecilus*
Species *P. maculatus*
Genus *Xiphophorus*
Species *X. helleri*
(*Lebistes* is included in family Poeciliidae by Regan, 1913)

LEBISTES

Lebistes, which is popularly known as the "Millions fish" and the "Guppy," is native in Venezuela, Trinidad, the Barbadoes, and has been introduced as a means of mosquito control in many localities such as Guiana, Panama, Jamaica, South Africa, etc. Since its first description as *Poecilia reticulata* by Peters in 1859, it has been assigned to various genera, *Girardinus*, *Acanthophacelus*, and is now best known as *Lebistes reticulatus* (Regan, 1913). It seems to have first appeared in Germany as an aquarium fish about 1905 (Wichand, 1906).

Lebistes has been shown by the work of Schmidt, of Winge and of Blacher to be remarkably adapted for genetic investigations. The color pattern is exceedingly variable in the males, and there is a rapid development so that sexual maturity is reached in from three to four months. There exists a striking dimorphism of sex. The female measures about 5 cm. in length and the male but 2.5 cm. The female is nearly uniformly pigmented—an olive brown color—while the male shows brilliant hues in varied combinations. This fish is viviparous, and the period of pregnancy is about thirty days. Details of the care of the fish are given by Winge (1927).

The first paper (Schmidt, 1920) dealing with the genetics of *Lebistes* revealed the existence of *Y*-chromosome inheritance, appearing only in males and transmitted only by males. A succession of later papers (Winge, 1922 b, 1923, 1927) have reported altogether the discovery of eighteen genes, of which only one is autosomal or non sex linked and seventeen are sex linked. Of these seventeen nine have thus far been restricted to the *Y* chromosome and three to the *X* chromosome, while five have been found to cross over between the *X* and *Y* chromosomes. This list has been modified by Blacher (1927, 1928) by subdividing two of Winge's genes into two and four genes respectively and adding one new gene. It should be borne in mind that the female, except in a few cases of sex reversal in old age (Winge, 1927; Blacher, 1926a and b), never exhibits the colors. She is known to transmit the color by progeny tests. The names and symbols of these genes are listed in table 1, and in figure 1 are shown in diagramatic form the color patterns of genes minutus, sanguineus, coccineus and vitellinus separately and in combination. In the original papers the patterns of all heritable characters are reproduced in color, and these must necessarily be consulted by anyone utilizing this type for genetic studies.

One notable result of these investigations and also of Aida's work on *Oryzias* has been the discovery of crossing over between the *X* and *Y* chromosomes. This is most clearly illustrated by the relationship of the genes maculatus and elongatus as described by Winge (1923). Maculatus is restricted to the *Y* chromosome and phenotypically it exhibits a black spot on the dorsal fin, a red spot below and in front of the same fin and a black spot (not always developed) in the anal region (fig. 2). Elongatus produces an elongation and a reddish yellow color on the dorsal and ventral edges of the caudal fin (fig. 2). As illustrated by figures 2 and 3 the gene *e* appears to cross from the *X* chromosome to the *Y* chromosome, which already contained gene *m*,

TABLE 1

TERMS AS GIVEN BY WINGE		ADDITIONS AND MODIFICATIONS BY BLACHER	NATURE OF PHENOTYPE	MODE OF INHERITANCE
Name	Symbol			
maculatus	(*ma*)		color character	*Y* chromosome
		macula rubia (m_r)	color character	*Y* chromosome
		macula nigra dorsales (m_{nd})	color character	*Y* chromosome
iridescens	(*ir*)		color character and silver sheen of side of body	*Y* chromosome
		bimaculatus (*bi*)	color character	*Y* chromosome and allelomorphic to *ru* complex (Blacher)
		variabilis—apparently not homologous with variabilis of Winge—causes yellow color in dorsal region of caudal fin (*va*)	color character	*Y* chromosome and allelomorphic to *ru* complex (Blacher)
		macula caudales (*mc*)	color character	*Y* chromosome and allelomorphic to *ru* complex (Blacher)
		anterior rubra (*ar*)	color character	*Y* chromosome and allelomorphic to *ru* complex (Blacher)
oculatus	(*oc*)		color character and form of caudal fin	*Y* chromosome
ferrugineus	(*fe*)		color character	*Y* chromosome
sanguineus (derived from ruber)	(*sa*)		color character	*Y* chromosome
aureus	(*au*)		color character and form of caudal fin	*Y* chromosome
armatus	(*ar*)	gladigerens (*g*)	color character and form of caudal fin	*Y* chromosome
		modified gladigerens (*g'*)	color character and form of caudal fin	*Y* chromosome
pauper	(*pa*)		color character	*Y* chromosome
variabilis	(*va*)		color character	*Y* chromosome
coccineus (derived from sulphureus)	(*co*)		color character	*X* chromosome
lineatus	(*li*)		color character and form of caudal fin	*X* chromosome
tigrinus	(*ti*)		color character	*X* chromosome
luteus	(*lu*)		color character	*X* and *Y* chromosomes
elongatus	(*el*)		color character and form of caudal fin	*X* and *Y* chromosomes
minutus (derived from ruber)	(*mi*)		color character	*X* and *Y* chromosomes
vitellinus (derived from sulphureus)	(*vi*)		color character	*X* and *Y* chromosomes
cinnamoneus	(*ci*)		color character	*X* and *Y* chromosomes
zebrinus	(*ze*)		color character	autosomal

thus producing chromosome *Yem* of which the inheritance may be traced. Gene *e* was also later found to cross back to an *X* chromosome. Other probable examples of crossing over have been noted, and in one case it has been a means of further analysis of the genetic complexes at first designated as genes sulphureus and ruber (Winge, 1922), which have been respectively subdivided into genes vitellinus and coccineus, and minutus and sanguineus (Winge, 1927). This was because certain portions of the color pattern of *su* and *ru* were observed to separate and cross over in inheritance. Those which showed crossing over were minutus and vitellinus, while coccineus remained associated with *X* and sanguineus with *Y*.

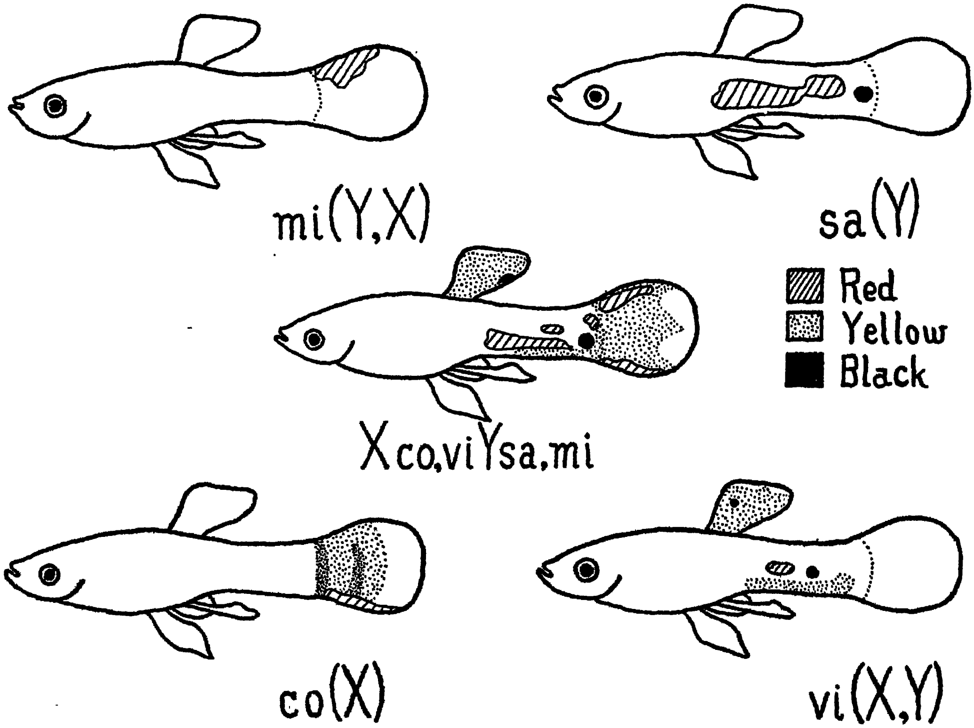

Fig. 1. Color Effects of Genes Minutus, Sanguineus, Coccineus and Vitellinus in Lebistes
Combined effect of all four genes shown in central figure. (After Winge, 1927.)

These investigations have raised several questions in regard to theoretical interpretation. Certain of the genes, such as sanguineus and coccineus, may be allelomorphs instead of occupying different loci in the chromosomes. The former is the type of interpretation adopted by Bellamy (1924, 1928) in his study of *Platypoecilus*, while Gordon utilizing the same material favors the concept of independent loci. Winge repeatedly refers to the *X* chromosome as being "empty," thus indicating his preference for the presence and absence hypothesis for this material. He finds no evidence that there exist active allelomorphs of the color factors and considers it possible that they may be non-existent. This concept is indicated in his formulae by the Symbol X_0. Blacher, however, (1928), considers that the genes derived from Winge's iridescens complex are allelomorphic to the sulphureus complex. A further point emphasized by Winge is that his evidence supports the idea that sex determination is controlled by a single pair of genes—a dominant factor for maleness resident in the *Y* chromosome and recessive factors for femaleness present in the *X* chromosomes. He considers that if genes for maleness

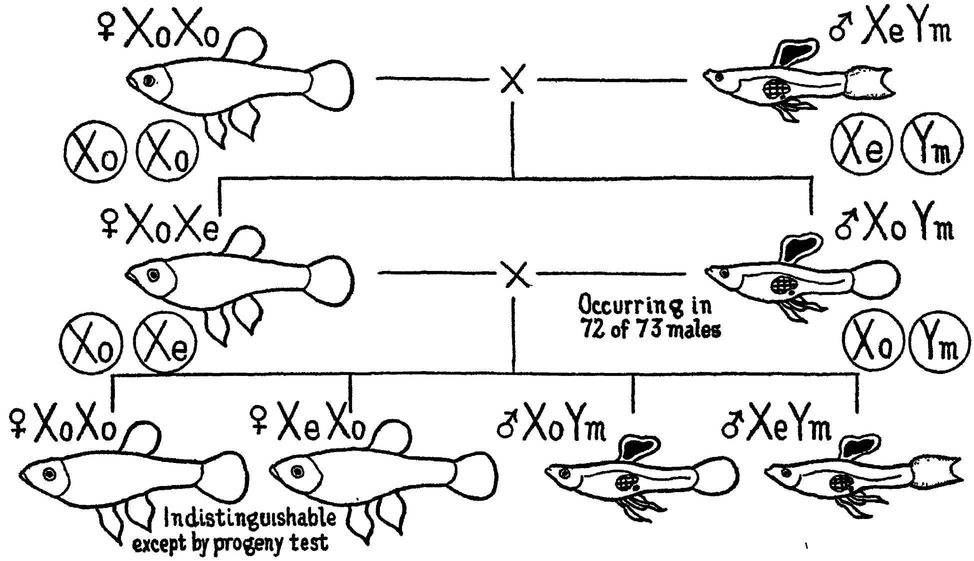

Fig. 2

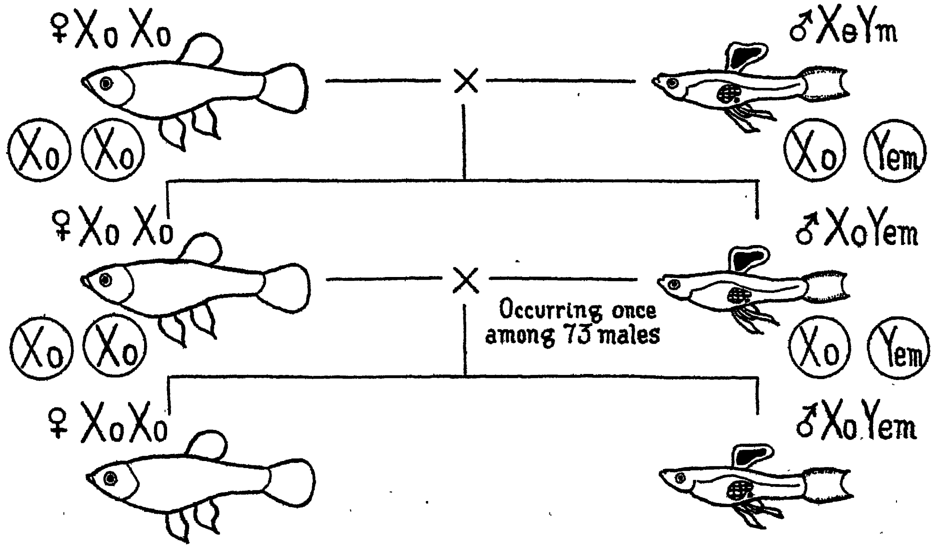

Fig. 3

Figs. 2 and 3. Y-Chromosome Inheritance and Crossing over in Lebistes

Fig. 2 shows *Y*-chromosome inheritance without crossing over. Fig. 3 shows the effect of a cross-over. Colors: Black, solid black; red, cross hatching; yellow, stippled. (After Winge, 1923.)

and femaleness were genetic complexes of many genes crossing over would take place and intersexes result. This latter sexual condition has not been observed in these fish. This interpretation has been criticized by Morgan (1924, 1926), who suggests that a number of genes for sex determination may be located in a part equivalent to a sex chromosome and the sex linked characters in a part that may be called an attached autosome. Under these conditions it would be necessary to add a secondary postulate to the effect that crossing over might occur in the autosomal section but not in the sex chromosome part.

TABLE 2

A. Genes and phenotypes in Oryzias (Aplocheilus)

GENE	PHENOTYPE
B	Pigment in black chromatophores highly developed
b	Pigment in black chromatophores slightly developed
B'	Pigment in about 50 per cent of chromatophores highly developed and in about 50 per cent slightly developed. Deeply pigmented chromatophores tend to group forming variegated pattern.
R	Pigment in yellow chromatophores highly developed
r	Pigment in yellow chromatophores slightly developed

B. Genetic constitution of varieties of Oryzias (homozygous condition)

PHENOTYPE	GENOTYPE
Brown (wild type)	*B B R R*
Red	*b b R R*
White	*b b r r*
Blue	*B B r r*
Variegated red	*B' B' R R*
Variegated white	*B' B' r r*

Demerec (1928), considering the situation in *Lebistes* from the point of view of his studies in the frequency of mutations, has suggested that it is highly improbable that almost all mutations should be limited to one of the twenty-three pairs of chromosomes (chromosome counts made by Winge, 1922a). He therefore suggests that instead of there being independent segregation many chromosomes may be associated in groups in reduction and that there may be occasionally breaks in this group which would account for crossing over. The situation would thus be similar to that found in a multiple *XY* chromosome group where an independent segregation might take place as was suggested by Goodrich (1926) in the study of an invertebrate type.

ORYZIAS

Of the genetic investigations on fish that by Aida (1921) is the most satisfactory with respect to the large counts obtainable and consequent definite results. As material he utilized the Japanese fresh water fish, *Aplocheilus (Oryzias) latipes*. This is a small fish (about 30 mm.) which is found wild in the ditches, pools and small streams of the ricefields of Southern Japan. This species has been referred to various genera, *Poecilia*, *Haplocheilus*, *Aplocheilus* and most recently was removed from this latter genus by Jordan and Snyder (1907) and placed in a new genus *Oryzias*. It is, however, best known to geneticists and to aquarists as *Aplocheilus* or to the latter by the common Japanese name Medaka. This is an oviparous or spawning fish. The eggs are carried for a short time on the underside of the body fastened to it by threads that are apparently formed in and attached to the walls of the oviduct. This characteristic is an advantage in genetic experiments as several females of different genotype may be left with a single male in an aquarium and there is no doubt as to the source of the eggs. Details of the care of the fish are recorded by Aida (1921) and Goodrich (1927). It appears that the normal period for attainment of sex-maturity is one year. The writer has, however, reared fish to maturity in six months, and it seems probable that by proper control of conditions two generations may be reared per year. The investigations of Aida on *Oryzias* were preceded by two less complete papers (Toyama, 1916; Ishiwara, 1917) and a reference to crossing experiments by Ishikawa (1913). This latter is the earliest publication dealing with Mendelian inheritance in fish that is known to the present writer. The species has been known to the German aquarists since 1897 (Bade, 1898).

Aida made a genetic analysis of certain color varieties—brown, red, white, variegated and blue. These he found to be due to the interaction of genes as indicated in table 2B. An inspection of these formulae show that B, B' and b form a series of multiple allelomorphs. In this series the genes are borne by autosomes, while the allelomorphic genes R and r are carried by the X and Y chromosomes. In Aida's experience an R gene was usually carried by the Y chromosome and r restricted to the X chromosomes. Hence white males were rare. The white males that did appear were the result of crossing over of the R gene from the X to the Y chromosome. Aida then shares with Winge (1922) in the independent discovery of Y-chromosome inheritance and of crossing over between X and Y chromosomes, which are the first examples of these phenomena to be described in any type.

TABLE 3

Di-hybrid cross in Oryzias showing Y chromosome inheritance and interaction of factors

Brown ♂	×	white ♀
$B\,B\,X_RY_R$		$b\,b\,X_rX_r$
Brown ♂		brown ♀
$B\,b\,X_rY_R$		$B\,b\,X_RX_r$

	$B\,Y_R$	$B\,X_r$	$b\,Y_R$	$b\,X_r$
$B\,X_R$	brown ♂ $B\,B\,X_RY_R$	brown ♀ $B\,B\,X_RX_r$	brown ♂ $B\,b\,X_RY_R$	brown ♀ $B\,b\,X_RX_r$
$B\,X_r$	brown ♂ $B\,B\,X_rY_R$	blue ♀ $B\,B\,X_rX_r$	brown ♂ $B\,b\,X_rY_R$	blue ♀ $B\,b\,X_rX_r$
$b\,X_R$	brown ♂ $B\,b\,X_RY_R$	brown ♀ $B\,b\,X_RX_r$	red ♂ $b\,b\,X_RY_R$	red ♀ $b\,b\,X_RX_r$
$b\,X_r$	brown ♂ $B\,b\,X_rY_R$	blue ♀ $B\,b\,X_rX_r$	red ♂ $b\,b\,X_rY_R$	white ♀ $b\,b\,X_rX$

Summary: Males: 6 brown, 2 red
Females: 3 brown, 3 blue, 1 red, 1 white

Aida also distinguished the various types of cells which were involved in the formation of the color pattern. These observations are discussed below in connection with developmental phenomena.

Table 3 gives an example of the mode of inheritance in *Oryzias* showing a typical case of dihybridism and the interaction of factors which yields an unusual ratio.

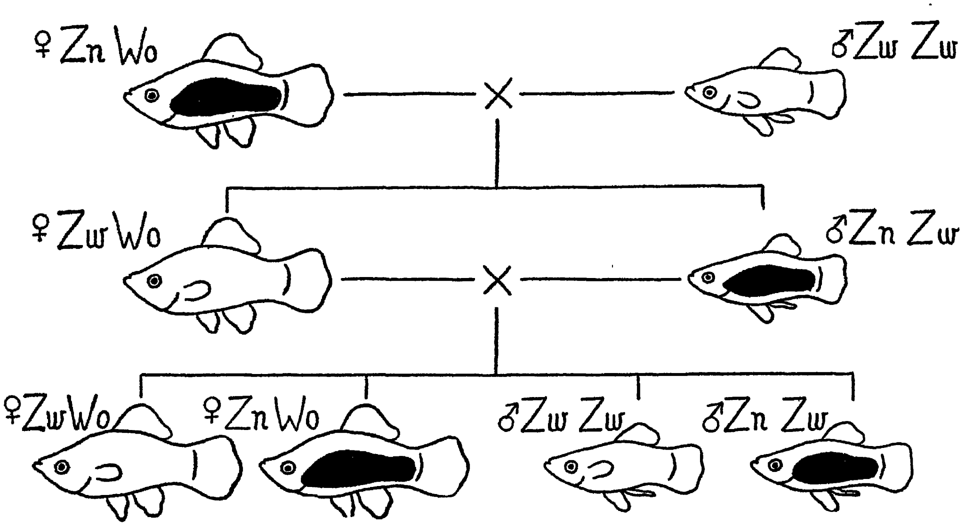

Fig. 4

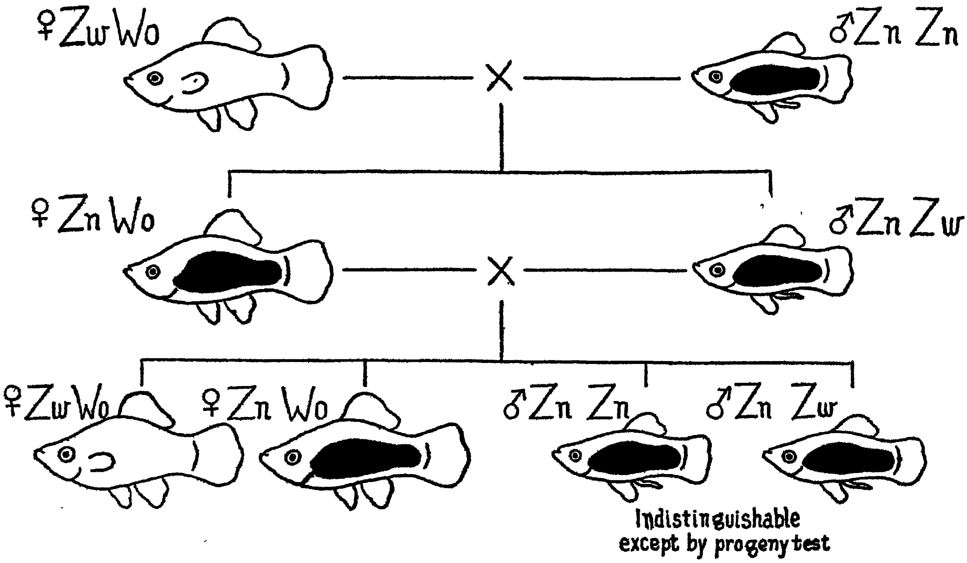

Fig. 5

Figs. 4 and 5. ZW Inheritance of Character Nigra in Platypoecilus

Fig. 4. Cross of Nigra female by white (Bellamy) or stippled (Gordon) male. Fig. 5. Cross of white (stippled) female by Nigra male. (After Bellamy.)

PLATYPOECILUS

Platypoecilus is a genus native in fresh-water streams and bayous of southern Mexico.

The species *P. maculatus* is remarkably variable in color pattern as noted by Meek (1904) from field collections and later by the German aquarists. An outline of the taxonomic history of this type is given by Gordon (1927). This fish is viviparous, the gestation period is about thirty days and sexual maturity of the female is attained in about eight months, but there is considerable variation. That of the attainment of male maturity is tabulated by Bellamy (1924). The color patterns have been variously named, and a list of fifteen is given by Gordon (*loc. cit.*). It is not surprising that this highly variable type should prove suitable for genetic investigations. A systematic study was first undertaken by Bellamy (1922, 1924, 1928), who has discovered sex linked characters which exhibit Abraxas or *ZW* type of inheritance in contrast to the conditions found in *Oryzias* (*Haplocheilus*) and *Lebistes*, where the Drosophila *XY* type prevails. Figures 4 and 5 illustrate the *ZW* type of inheritance. Gordon (1926, 1927) has made an independent genetic analysis of *Platypoecilus* confirming Bellamy's finding of the *ZW* type of inheritance but also adding the autosomal character stippled; he is in disagreement with Bellamy in regard to certain details. It is well to keep in mind in regard to *Platypoecilus* that the various varietal names given by systematists and aquarists should not be confused with designations of analyzed Mendelian characters. Thus the red variety, or Rubra, a red "platy," involves factors for "spots, stipples and *red*." The following table (4) is an attempt to harmonize the present nomenclature. Of the genetic factors *St* and its allelomorph *st* are autosomal, while all others are sex linked and carried by the *ZW* chromosomes. Bellamy regards these sex linked factors as constituting a series of multiple allelomorphs such that males may be homozygous or may carry any two of the genes *R*, *N*, *P*, *W*, etc., while the female, being the heterogametic sex *ZO*, will carry only one gene of the assortment. Fraser and Gordon (1928, 1929; the authors have kindly allowed the pres-

TABLE 4

Terminology of Platypoecilus

TERMINOLOGY BASED ON THAT GIVEN BY AQUARISTS	TERMINOLOGY SUGGESTED BY GORDON 1927	GENETIC SYMBOLS	
		Bellamy	Adapted from Gordon 1927
Rubra	Red-platy	*R*	*R*
Nigra	Black-platy	*N*	*N*
Pulchra	Spotted-platy	*P*	*Sp*
White (Bellamy 22)	Stippled-platy	*W*	*St*
Immaculatus	Gold-platy		*r, n, sp, st*

According to Gordon the Rubras or Red-platys of aquarists usually have other factors present, namely: RR SpSp StSt.

The Nigras or Black-platys usually have Stipples, thus: NN StSt.

The Gold-platy is a multiple recessive.

Chromatophores of Platypoecilus from Gordon (1927)

	RED	SPOTTED	BLACK	STIPPLE	GOLD
Melanophores					
a. Stipples	+	+	+	+	−
b. Spots	+	+	+++	−	−
Erythrophores	+	−	−	−	−
Xanthophores	+	+	+	+	+

ent writer to refer to their paper while in press), however, found evidence which indicates that there may be present a gene-carrying *W* chromosome into which genes may cross over from the *Z* chromosome. A second conclusion of Fraser and Gordon, based on an apparent crossover, is that genes for red color and spotting should not be considered allelomorphic but rather occupy closely adjoining loci on the paired chromosomes, so that the preferred formula for a heterozygous male is *Rsp*, *rSp* rather than *R*, *Sp*. This interpretation is followed in table 4. It is possible that further work will indicate that *N* (Nigra) should also be considered as a closely linked gene rather than as an allelomorph of *R* and *Sp*.

The color patterns in *Platypoecilus* are produced by the development of various chromatophores as indicated by the following table (4, from Gordon). It is interesting to note that here is indicated in most cases a relation between the genes and definite types of cells and in one case (Black) an effect of the arrangement or massing of the cells to produce a broad black band on either flank of the fish.

CARASSIUS

The goldfish, *Carassius auratus*, is the earliest known of ornamental fish here discussed. Chen (1925) in his review of the old Chinese literature finds that the red scaled fish were reported observed during the Tsin dynasty (265–419), but they were not domesticated until the Sung dynasty (960–1278). The taxonomic designation is now applied both to the ornamental and to the wild or brown form, which is native of China but has been elsewhere introduced.

The practice of goldfish culture is of course well understood. One of the best manuals is that of Innes (1921). (See also Fearnow, 1925). In spite of the familiarity of the goldfish and the abundance of varieties little progress has been made with any Mendelian analysis until the present year. The delay has probably been due to the necessity of more extensive facilities—outdoor pools, etc.,—and the longer time required for attainment of sexual maturity (two years is usually considered the minimum). Hance (1924) in a brief note reports the probable dominance of red and black over white, of normal tail over double or fantail and of normal eyes over the telescope variety. No ratios are reported.

Chen's paper (1928) appears to be the first Mendelian analysis that has been made. He has studied the inheritance of certain characters found in the ordinary goldfish and the "Scaleless" varieties, of which the type known to fanciers, Shubunkin, is an example. The so-called "Scaleless" types have scales, but they are transparent and hence almost invisible on account of the absence in the scales of a layer of reflecting crystals, the guanin, which gives the silvery sheen to the sides and belly of many fish. This material may be present in one or more layers—in some cases one underlying and another in the scales.

The investigations by Chen show that the scaled and "scaleless" characters are allelomorphic, and he has designated the genes as *T* (scaled) and *T'* (scaleless). Differences in development of the reflecting layer are also accompanied by characteristic pigmentation. The effect of the genes may be stated as follows: Gene *T* (homozygous) produces several layers of reflecting tissue including that in the scales, and black and yellow chromatophores are abundant. Gene *T'* (homozygous) causes a reduction of reflecting tissue until it is nearly or wholly absent. The black chromatophores are restricted to an area at the base of the caudal fin and the yellow chromatophores are absent. The heterozygous types *TT'* reveal a condition of incomplete dominance. The reflecting tissue is present in varying degree—on the head, a portion of the deeper layer over the body, in isolated scales (from 2 to 14) or combinations of all. The black and yellow chromatophores are both present but so arranged as to give a characteristic mottled color effect—that of the Shubunkin.

It thus appears that the Shubunkin of the breeders is a heterozygous type, which it is impossible to perpetuate as a pure stock. The homozygous scaleless types are usually weaker and less abundant. If, however, this race is maintained and bred with scaled types, the Shubunkin is always produced.

RIVULUS

The form which has most recently entered the lists for genetic investigation is *Rivulus urophtalmus*. A brief note by Constantinescu (1928) indicates the dominance of a black color phase over a red phase. This pair of allelomorphs is apparently autosomal.

SPECIES HYBRIDS

Thus far the interspecific hybridization of fish has been of greater importance in the study of certain phases of the mechanism of development than in the study of inheritance. That is, such experiments have yielded results bearing on the relation of chromatin to development, of controlling factors in ratio of cleavage and in the process of gastrulation. Almost all of these crosses have been between types of which no Mendelian analysis had been made. There has, therefore, been no possibility of tracing the effects of individual genes. Since hybridization among fish has had a considerable degree of success, it seems probable that as our knowledge of Mendelian inheritance in fish increases such observations will become possible.

Two sorts of studies have been made—those dealing with the phenotypic effects of the hybridization and the studies of the behavior of chromatin in hybrids. There have been numerous accounts of hybridization or alleged fish hybrids which are of little value (see Dean, *Bibliography of Fishes*, Vol. 3, pp. 505–507 for references). The earliest of the more accurate observations were those of Appellöf (1894) and Moenkhaus (1904). The former made crosses between Cod and Flounder, Cod and the European Cunner, the Dab and Flounder, and between two species of stickleback. In some crosses development stopped at the conclusion of cleavage and in others when the embryo was fully formed. Moenkhaus crossed *Fundulus heteroclitus* and *Menidia notata*. In both of these cases there is little information bearing on the relative effect of either parent except on cleavage stages and gastrulation. The work of Moenkhaus is notable in showing that the chromosomes of both parents were present in nuclei and were fully mingled. Further studies of chromosome behavior have been made by Morris (1914), P. and G. Hertwig (1914), and Pinney (1922, 1928). A review of chromosome behavior in hybrids has been made by Morgan (1927). Bancroft (1912) has made a careful analysis of the history of chromatophores in hybrids of *Fundulus majalis* and *Fundulus heteroclitus*. He finds that certain characteristics of pigment cells in *F. heteroclitus* are dominant over the condition found in *F. majalis*, while on the other hand in regard to certain features of the time of development of chromatophores he finds a "blending" or intermediate condition. Newman in an extensive series of papers (1914, 1915, 1918) has shown the possibilities of many teleost hybridizations. Some hatch, many do not. He describes many instances of varied effects of hybridization—dominance, blending, mosaic conditions. Essentially similar results have been obtained by Paula and Gunther Hertwig (1914) in fish from the Gulf of Naples.

TABLE 5

Xiphophorus helleri (*strigatus*) × *Platypoecilus maculatus*

Inheritance of coloration

			HYBRID CHARACTERS	
			Male	Female
(1) Gerschler (1914)				
X. strigatus female	×	*P. maculatus* male	Xiphophorus characters	Xiphophorus characters
(2) Kosswig (1928)				
X. helleri female	×	*P. maculatus* male var. black platy	57 black 25 red	5 black 42 red
			(total 62 black 67 red)	
(3) *X. helleri* female	×	*P. maculatus* male (gold platy)	21 red	17 red
(4) *X. helleri* female	×	*P. maculatus* male (red platy)	28 red with black flecks 22 black (sex not determined)	
(5) Innes (1921)				
X. helleri female	×	*P. maculatus* male (red platy)	Red, black splotches both sexes	
(6) Kissel. Reported by Mellon (1928)				
X. helleri female	×	*P. maculatus* male (red platy)	1 red male, 49 mottled (black splotches?) both sexes	
(7) Haffner (1913). Reviewed by Gerschler (1914)				
P. maculatus female	×	*X. helleri* male	Platypoecilus characters	Xiphophorus characters

Some of the most interesting cases of species hybrids of fish have been discovered by the aquarists. The best known of these are the crosses between *Xiphophorus helleri* and the varieties of *Platypoecilus maculatus*. Most matings have been between *Xiphophorus* female and *Platypoecilus* male. In many respects the hybrids are intermediate between the parental types. In regard to coloration there is some evidence of segregation. This is summarized in table 5. It is possible to tentatively harmonize these somewhat diverse results by assuming that in crosses (2) and (4) *Platypoecilus* was heterozygous for factors affecting melanophore development, in (1) and (3) homozygous for absence of Nigra and spotting, and in (5) homozygous for spotting. The most striking result is that obtained by a backcross from the F_1 (5) with *Xiphophorus helleri* male. This gives a vigorous hybrid larger than either parent and having a brilliant red color. (See Innes, 1921, pp. 68–69; and Mellon, pp. 89–90). It may be that genes which affect the red chromatophores have been received from both parent species.

Various crosses have been made by the aquarists. See Schreitmüller, 1925 (*Danio rerio* × *Danio albolineatus*), 1926a (*Xiphophorus helleri* female × *Lebistes reticulatus* male, *Xiphophorus helleri* female × *Mollienesia formosa* male, *X. helleri* male × *Mollienesia velifera* female, *X. helleri* female × *Limia arnoldi* male, *Xiphophorus helleri* female × *Limia nigrofasciata* male, *Xiphophorus helleri* female × *Phalloceros caudomaculatus*), Schreitmüller, 1926b (*Brachydania rerio* × *Danio malabaricus*), Schreitmüller, 1926c (*Gambusia holbrooki* female × *Cnesterocdon decemmaculatus* male), Meinken, 1925 (*Danio albolineatus* male × *Danio analipunctatus* female). These papers give but brief descriptions of the experiments but they are suggestive of the possibilities for more critical analysis. Embody (1918) has described hybrids obtained by artificial insemination between pike and pickerel and Phillipps (1922) gives an account of crosses between two species of salmon from Australia. These reports seem to indicate that fish are more favorable than most other animal forms for this type of experimentation.

SEX DETERMINATION AND SEX DIFFERENTIATION

The phenomena of sex determination and sex differentiation are essentially one part of the larger problem of the relationships between the genes and the physiology of development. It is a part, however, which has thus far been more completely analyzed and in which the complexities of the situation are most clearly revealed. It seems probable that studies on fish may yield data of importance bearing on these problems. The fact that both *XY* and *ZW* types of inheritance are found in closely related fish such as *Lebistes* and *Oryzias*, *XY*, and *Platypoecilus*, *ZW*, is of some significance in considering the evolutionary origin of these conditions. The existence of this situation in *Lebistes* has led Winge (1923, 1927) to the opinion that there is present a single pair of genes—a recessive for femaleness borne by the *X* chromosomes and a dominant gene for maleness borne by the *Y* chromosome. This is obviously a concept sharply at variance with that held by most workers on *Drosophila*.

Harms (1926) has crossed normal females of *Xiphophorus helleri* with males that have attained their sex after reversal from the female condition. His results though limited are in accordance with the hypothesis that there exists in these types an *XY* complex and that in sex reversal the original sex formula is retained. Thus in the above cross an *XX* female is mated with an *XX* male and as expected under these conditions all offspring are female.

The work of Essenberg (1923, 1926) shows that sex reversal is normal in *Xiphophorus*. There is a great preponderance (74 per cent) of females among the young fish, but later the sex ratio is reversed, giving 75 per cent males. It is not known how widely such cases of sex reversal may occur among fish. Geiser (1924) gives a tabulation of sex-ratios among fish.

Conditions of sex reversal naturally suggest investigations of the relation of secondary-sex characteristics to the gonads. Blacher (1926) and Frazer and Gordon (1929) have noted a correlation between testes development and appearance of male colors. The most extensive studies are those on *Gasterosteus* and *Xiphophorus*, by van Oordt (1924, 1925), who considers that there is a correlation between the development of male sex cells and secondary sex characters and that the interstitial cells of the testes play no part in internal secretion. This conclusion is in accord with that of Champy (1923) but quite the reverse of that of Courrier (1922). Very little experimental work of removal of gonads has been done. Kopec (1927) performed castration experiments on the fish *Phoxinus laevis*, after which some failed to assume the nuptial hues. They did not however live more than three weeks after the operation.

CHROMOSOMES

Fish have proved to be notably difficult material for study of chromosomes. Winge (1922a) records the haploid number of 23 from *Lebistes*. Goodrich (1927) finds haploid counts in *Oryzias* (*Haplocheilus*) varying from 22 to 24. The fact that fish are not favorable for cytological investigations is the most serious drawback for their use as material for genetic studies.

DEVELOPMENT

It has been suggested above that fish are likely to prove favorable material for studies bearing on the development of genetic characters. This is because the embryology of fish (especially the oviparous or spawning types) can be much more readily studied than that of other vertebrates. The egg is often transparent, the development is rapid and the embryo is not hidden by egg shell or enclosed within the body of the parent. The development is relatively simple and free from complications of metamorphosis such as are present in insects.

The embryonic and later history of the Mendelian characters described by Aida (1921) for *Aplocheilus* (*Oryzias*) *latipes* have been in part traced by Goodrich (1926, 1927). As the characters involved are color varieties the paper presents a study of the pigment cells or chromatophores. The phenotypic condition induced by the various genes is indicated by table 2. Herein it is indicated that in all phenotypes all pigment cells are present but the development of the pigment in these cells varies with the different types, though counts of chromatophores indicate that the same number of these cells is present in all cases. Hence it is apparent that the Mendelian character is not, in this case, produced by "energy of division" of cells (such as a greater multiplication of black chromatophores in the brown type) but rather by some other mechanism operating upon or within a constant number of cells. Observations on the young and embryonic stages confirm this concept. That this effect can not be due solely to an extracellular agent (such as a hormone) is shown by the conditions in the variegated type where some black chromatophores are heavily pigmented while in neighboring cells little pigment is developed. The conditions suggest that at an early stage there may be an embryonic segregation of anlage for deeply and for lightly pigmented cells and that they then migrate to form the color pattern of the variegated type. That the segregation must occur very early in development is indicated by the fact that Mendelian ratios may be obtained within two days after fertilization at about the stage of nine somites. Gordon (1927) in his analysis (see table 4) indicates clearly the cellular effect of different genes. The chromatophores primarily influenced by genes *Sp*, *St*, *R* are quite distinct. In the case of *Sp* and *St* there are two different types of black chromatophores differing in size and in form. In goldfish it is possible that a quite different mechanism for color production prevails. Chen (1928) reports that in them there is a complete absence of yellow chromatophores and a great reduction of melanophores in the homozygous shubunkin, though Fukui (1927) reports that the varied colors of many goldfish are produced by the actual disintegration of pigment cells after a full complement was formed in the young stages.

Further complications are indicated by the phenomena of sex-reversal in fish as described by Blacher (1926), Winge (1927), and Essenburg (1923, 1926). In these cases there is clear indication that the action of hormones brings out the characteristic male color pattern. It seems to the writer highly improbable for reasons mentioned above in connection with the observations on the chromatophores in variegated *Oryzias*, that hormones alone can produce color pattern because their distribution is likely to be uniform through the blood stream, but a hormone acting on differing groups of cells might have such an effect. A complete understanding of these examples of coloration in fish would go far toward solving many problems of color pattern.

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THE CHEMICAL SENSES OF INSECTS

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JUST as the vertebrates are so frequently creatures of their visual and auditory senses, so the insects are largely creatures of their chemical senses. For it is chiefly by means of these senses that most insects find their food, their mates, and the food of their offspring, and that the social insects are enabled to make the manifold sensory discriminations necessitated by their highly complex social organization. It is not surprising, therefore, that this subject has received considerable attention. Indeed, in view of its importance, the surprising thing is that it has not received more attention.

The chemical senses of the vertebrates are separable into three clearly distinct categories, smell, taste, and the common chemical sense, each of which in turn appears to be capable of further resolution into a greater or lesser number of distinct senses (Parker, 1922). These categories are more or less closely related, and the distinctions between them have not always been clear. Thus, some of the earlier physiologists attempted to draw a distinction between smell and taste in the air breathing forms on the basis of the physical condition of the stimulus. For smell, the stimulus was thought normally to be a gas; for taste, a solution. Gradually, however, it became clear that in the case of the olfactory stimulus the gaseous particles, in order to reach the free ends of the sensory cells, must pass through the mucous solution in which these are enveloped. In other words, the gas must enter into solution. The situation is similar for the common chemical sense. In the vertebrate, therefore, the physical state of the adequate stimulus for all three groups of chemoreceptors is identical, viz., a solution of "chemically active material," in direct contact with the surface of the sensory cell (Parker, 1922, p. 168).

SMELL, TASTE, AND THE COMMON CHEMICAL SENSE

There are, nevertheless, certain characteristics by which these three categories of chemical sense may be differentiated. First, they differ with respect to anatomy and to distribution in the body. Second, they differ to a considerable extent with respect to the general classes of chemical materials which stimulate them. This is especially clear when smell and taste are compared. As Parker (1922, p. 170) remarks, "what is smelled is generally not tasted and what is tasted is not smelled." Third, they differ with respect to their threshold concentrations. This is well illustrated by the experiments of Parker and Stabler (1913) with ethyl alcohol, a substance which affects smell, taste, and the common chemical sense in man. The threshold for smell was found to be 24,000 times lower than that for taste, which in turn was 2 or 3 times lower than that for the common chemical sense.

Fourth, they differ with respect to the rôles played in the economy of the organism. Smell is usually concerned with directing the animal to a more or less distant source of stimulation,—food or a mate; taste, largely or solely with digestive reflexes, in the broad sense; the common chemical sense, with the detection of substances which are irritating and, hence, unfavorable to the animal's well being.

Whether the insect, like the vertebrate, possesses clearly distinct senses of smell and taste has been a matter of some discussion. Thus, McIndoo (1916, 1926) is of the opinion that in insects there is no true sense of taste and that apparent taste discriminations are to be attributed to a very highly developed sense of smell. This opinion is based on morphological work on the honey bee and the cotton boll weevil, in both of which he failed to find sense organs on the mouth parts which appeared to him suitable for organs of taste. The only sense organs found were various types of innervated hairs and the organs which have been named by him "olfactory pores." The first of these he believes to be anatomically unsuited to chemical stimulation. The second he finds to be identical in structure with the olfactory pores located elsewhere on the body, to which he attributes an olfactory function. As will be shown subsequently, however, recent work (Minnich, 1926b; v. Frisch, 1927) substantiates the viewpoint that there is quite as much ground for separating smell and taste in the insect as there is in the vertebrate.

Whether in addition to smell and taste the insect possesses something comparable to a common chemical sense, cannot be stated at present with certainty. Insects do respond to irritants, but the nature of the receptors concerned is not yet clear. The preliminary experiments of Hartwell (1924) may indicate a set of receptors for irritants, distinct from the olfactory receptors. Further experimentation must, however, determine this question.

WHERE ARE THE OLFACTORY ORGANS OF INSECTS LOCATED?

By far the greater part of the work on the olfactory sense of insects has been directly or indirectly concerned with the location of the sense organs and the determination of their structure. Many years ago Forel (1908, p. 74) opened a discussion of the olfactory sense in insects by saying that so much had been written on the subject that it was almost like gilding refined gold to return to it. Nevertheless, a great deal has been added to our knowledge of this subject since Forel wrote, and there is undoubtedly a very great deal yet to be learned.

During the eighteenth and the earlier part of the nineteenth centuries, the olfactory organs of insects were assigned by different writers to various locations, including the spiracles, the tracheae, and almost every conceivable location on the head and its appendages (cf. McIndoo, 1914c). Toward the end of the nineteenth century, however, through the work of Forel (1908), Hauser (1880), and others, the antennae came to be generally accepted as the seat of the olfactory sense. A summary of the evidence which led to this conclusion is given by Forel. In so far as the evidence was experimental it consisted in observing the responses of various insects to odors before and after antennal elimination, the antennae being eliminated either by amputation or by being covered with some presumably impervious material.

A rather striking experiment carried out by Mayer (1900) on the moth *Promethea* deserves especial mention in this connection. Having shown experimentally that the males of this species are attracted to the females solely by chemical means, Mayer carried out various operations on the males. He found that males with the entire abdomen removed were still attracted to the female in normal fashion. If, however, the antennae of a male were covered with an impervious layer of photographic paste, it no longer sought the female nor displayed any excitement even when placed within an inch of her. In five such animals the paste was subsequently dissolved off with water, with the result that four of them "readily mated with the females." Upon again covering the antennae, however, "the males again failed to notice the females." Experiments of this sort certainly constitute very convincing evidence in favor of the antennae as seats of olfactory sense.

THE EXPERIMENTS OF VON FRISCH

Further evidence on this question has recently been afforded by the brilliant work of the German physiologist, v. Frisch (1921), on the honey bee. At a favorable spot out of doors, this investigator set up an experimental table on which was placed a row of four small cubical porcelain boxes, each provided with a circular entrance, 1.5 cm. in diameter, near the bottom of one face. Three of these boxes were empty and odorless. The fourth by virtue of a few drops of an oil placed inside was filled with a flowery odor, which emanated through the opening to the outside. This box also contained a dish of sugar water. By gradual steps, bees were trained to come to the table and to enter the odorous box in search of the sugar water. Each bee thus trained was marked on the thorax with a fleck of paint of a different color, by means of which careful records of the behavior of each individual could be kept. Frequent changes in the position of the odor box with respect to the others soon showed that the bees always went directly to the odor box. An association, quite independent of the position of the box, had thus been established between the odor and the presence of food.

After a few bees had been thoroughly trained, a period requiring about one hour, they were carefully caught, and the two antennae amputated. So skillfully was the whole procedure carried out that it apparently disturbed the bee very little, for immediately upon release she resumed her search for the odor box. While the operation was in progress, however, the four old boxes were replaced by four new ones, three of which were again odorless and empty, while the fourth carried the odor but lacked the sugar water. The odor box was also shifted to a new position in the row. The bees without antennae now hovered in front of first one box, then another, and entered the odorless boxes as frequently as, or more frequently than, the odor box.

In answer to the objection that the results might be due to the shock of operation rather than to the loss of specific sense organs, v. Frisch carried out an ingenious check experiment, using color instead of odor. The front of the box containing sugar water was covered with blue paper; the front of the empty boxes, with yellow paper. Removal of the antennae of animals trained to blue, however, failed to alter in the slightest degree the association with color. In every other respect, too, he reports that the behavior of the bees appeared to be normal. The ability to distinguish odor alone was gone. These results, together with the results of other more or less similar experiments, led v. Frisch to conclude that the olfactory organs must be located on the antennae.

In order to discover more exactly the location of the sense organs concerned, various experiments were carried out in which only portions of the antennae were removed. The results showed that so long as the fourth flagellar segment of one antenna remained intact, the bees could still distinguish an odor to which they had been trained or even be trained to a new odor. Indeed if only the proximal three-fourths of this segment remained there still persisted clear traces of olfactory discrimination for a time after the operation. With the complete elimination of this segment, however, olfactory discrimination disappeared.

THE PORE PLATES

Morphological study of the antenna with particular reference to this segment showed that the organs concerned were the so-called pore plates. The chitinous outer portion of these sense organs consists of a thick, oval plate surrounded by a narrow ring which is exceedingly thin. The sensory fibers terminate under the thin ring and not under the thick central portion, as previously thought. Hence the sense organs are structurally suited to the reception of chemical stimuli. The morphological as well as the experimental evidence thus indicates that the antennal pore plates of the honey bee are olfactory receptors. Von Frisch also considers the sense cones of the antennae to be olfactory in function. More recent morphological studies of the antennae of Hymenoptera in general (Vogel, 1923; Wacker, 1925) have borne out these conclusions and have shown that the antennal end organs of olfactory sense in this group include pore plates, cones, and hairs.

Working on the location of the olfactory organs in termites, Hartwell (1924) tried the effect of applying local anaesthetics to the surface of the antennae of these animals. Although her experiments were carried out on such a small number of individuals that they are little more than suggestive, they seem to indicate a loss of the olfactory sense after anaesthetization of the antennae.

Indirect evidence of the antennae as seats of olfaction has also been furnished by Liebermann (1925). In a comparative study of the antennae of the muscid flies this investigator was able to show a definite correlation between the number of sense organs on the antennae and the olfactory requirements of the insect. Thus, the antennae of flies that obtain their food from flowers, which are present in profusion throughout the breeding season and which are readily distinguished visually, were found on the average to have only 494 sense cones in pits and 1478 on the surface. The antennae of flies feeding on filth, carrion, and dung, substances which are more occasional and less widely distributed in nature and which are difficult or impossible to distinguish visually, had on the average 820 pit cones and 2764 surface cones, or nearly twice as many as the first group. Finally, the antennae of *Oestridae* or bot-flies, in which the connection between the insect and its food supply is even more tenuous, had 4683 pit cones and 1700 surface cones.

THE OLFACTORY PORES

The more recent investigators, however, have not been unanimous in their opinion as to the location of the olfactory sense organs. In a series of publications beginning in 1914, McIndoo (1914a, 1914b, 1914c, 1915, 1917, 1918, 1920a, 1920b, 1926) has attempted to show two things: first, that the antennae are not the seat of the olfactory organs; and second, that the latter are the structures called by him "olfactory pores," which are located chiefly on the wing bases and the proximal portions of the legs, but also in small numbers on various other parts of the body.

In support of these contentions McIndoo offers the following arguments:

1. In the antennae the distal ends of the sensory terminals are covered with chitin, whereas in the olfactory pores they are exposed to the air. Hence, the latter are better suited to the reception of chemical stimuli than the former.

2. Any operation on the antennae renders the animal abnormal, so that failure to respond following this may be due to the general effect of the operation rather than to the elimination of olfactory organs. A measure of normality in behavior is post-operative longevity.

3. The reaction time (that is, the time required for a quiet animal to make any movement) to essential oils and other odorous substances is not significantly changed by eliminating the antennae, but it is greatly prolonged by eliminating the olfactory pores of the wing and leg bases.

To each of these arguments, serious objections may be offered. Concerning the actual penetration of the chitin by the sensory terminals of the olfactory pores, it may be said that most insect histologists believe that the outer chitinous layer is broken at no point. It may be exceedingly thin, as thin as half a micron over certain sensory terminals according to Snodgrass (1926), but it is always present. Furthermore, Eidmann (1922) has shown experimentally that chitin is not impervious at least to such substances as acids and alkalis. The evidence, therefore, seems to favor the view that all chemoreceptors are covered with at least a thin layer of chitin, through which the stimulating material must pass to reach the sensory terminals, rather than that the latter are exposed.

That any antennal operation renders the behavior of the animal so abnormal as to be unreliable, seems likewise not to be borne out by the facts. The work of v. Frisch (1921) on the honey bee, on which McIndoo did much of his work, certainly does not corroborate this. As v. Frisch points out, one may remove the eight distal segments of one antenna and the seven distal segments of the other, a total of fifteen segments, without the loss of such olfactory discrimination as his experiments demanded. But if the eight distal segments are removed from both antennae, a total of sixteen segments, olfactory discrimination is gone. The difference in the results following these two operations can scarcely be due to a difference in the extent of injury or shock. Nor is the idea that antennal elimination is always followed by marked abnormality of behavior, as indicated by short post-operative longevity, borne out by recent work. In some experiments with the cabbage butterfly, which I undertook a few years ago (Minnich, 1924), several individuals lived for about three weeks following antennal removal, and Abbott (1927a) has recently reported Necrophorus beetles still alive, six weeks after the same operation. In view of these facts, I do not believe that we are warranted in attributing the lack of response following antennal elimination to general abnormality of behavior.

The third argument mentioned is based on length of reaction time. According to McIndoo there is an inverse relation between the number of olfactory pores present and the average reaction time to odors. The following examples will illustrate the point for the honey bee. The odorous substances employed were oil of peppermint, oil of thyme, oil of wintergreen, honey, pollen, and leaves and bits of stems of pennyroyal. Drones were found to have 2600 olfactory pores, and an average reaction time to these six odors of 2.9 seconds; workers, 2200 pores, and a reaction time of 3.4 seconds; queens, 1800 pores, and a reaction time of 4.9 seconds. Similar results were obtained when various groups of olfactory pores were eliminated by one means or another. Thus, in the worker the pores located on the wing bases constitute two thirds of all the pores present in the body, and their elimination increased the reaction time about eight times. In contrast to these results, it was found that the elimination of the antennae, which lack "olfactory pores," failed to alter the reaction time appreciably. From such results, McIndoo argued that the "olfactory pores" must be olfactory organs.

From a physiological viewpoint it is easy to understand how a difference in the number of sense organs might be correlated with a difference in the degree of responsiveness. In other words, the more sense organs the insect possessed the more vigorous its response to a given stimulus might be. But it is certainly difficult to see why differences in the number of sense organs present should be correlated with differences in the time of response. The point in question is illustrated by an observation made by Crozier (1915) on chemical stimulation of the skin of the frog. Crozier found that the time required for a spinal frog to withdraw its foot from a salt solution was essentially the same whether the entire foot or only one half the length of the digits was immersed.

OLFACTORY ORGANS NOT CONFINED TO THE ANTENNAE

McIndoo's evidence, therefore, fails to show conclusively either that the antennae are not the seats of the olfactory organs or that the olfactory pores are the olfactory organs. This does not mean that the so-called olfactory pores may not be olfactory in function. They may be, but the evidence available is not conclusive on the point. One fact is, however, clearly brought out by McIndoo's experiments, namely, that insects still respond to the odors of essential oils after the elimination of the antennae, or of the olfactory pores. Nearly fifty years ago Hauser (1880) noted that certain beetles and certain Hemiptera still responded to such odors as turpentine and carbolic acid, after amputation of the antennae. Recently Hartwell (1924) has shown for termites, and Abbott (1927a) for certain common beetles, that there is a persistence of response to essential oils after the antennal elimination. The beetles employed by Abbott still responded after the elimination of the antennae and of the olfactory pores on the wing and leg bases. In all of these cases the stimuli used may have acted as irritants, and may have affected the animal through other sense organs than the olfactory organs.

McIndoo's bees, however, also responded to honey and pollen after antennal elimination. Other instances have also been reported indicating the persistence of olfactory discrimination after the complete elimination of the antennae. Using the extension of the proboscis as an indication of olfactory stimulation, the writer carried out some experiments with the cabbage butterfly (Minnich, 1924). After twenty to thirty hours of total inanition, these insects were found to become regularly responsive to appropriate odors. If one antenna was amputated, the response decreased about 6 per cent. If the remaining antenna was amputated there was a further decrease of 46 per cent, or a total decrease of 52 per cent. Experiments in which the antennae were covered with vaseline or a paraffin-vaseline mixture gave similar results. The elimination of the antennae thus decreased the response but failed to abolish it.

The results obtained by Abbott (1927a) on carrion beetles are similar. Beetles without antennae located and dug up decaying meat or cloth soaked in skatol, buried in the sand of the box in which they were kept. One individual of *Necrophorus americanus*, which had neither antennae nor wings, and in which the leg bases were covered with shellac, invariably found the meat within a few hours. There can be little doubt, therefore, but that olfactory organs are present elsewhere than on the antennae. Just where these organs are located and what their structure may be, is not known. They may be organs on the mouth parts; they may be the olfactory pores of McIndoo; or they may be still more widely scattered sense organs. Abbott (1927 a, b) has recently expressed himself as favoring the last of these viewpoints, viz., a general distribution over the surface of the body. In any event, it is becoming increasingly clear that although olfactory organs are present on the antennae they are not confined to these appendages.

THE PHYSIOLOGY OF OLFACTION

There has been a great deal of scattered work on the attraction of insects by odorous substances, most of which has been directly inspired by economic problems. Without attempting to review this literature, several of the papers dealing with the broader physiological aspects of this problem may be mentioned briefly. Barrows (1907) worked on the chemical substances responsible for the attraction of *Drosophila melanogaster* to its food, viz., fermenting fruit. Of a number of substances tested, the flies responded significantly to five: amyl alcohol, ethyl alcohol, acetic acid, lactic acid, and ethyl acetate, all of which occur in fermenting fruit. Under the conditions of the experiment the optimum concentration of ethyl alcohol was 20 per cent, and of acetic acid, 5 per cent. A mixture of $2\frac{1}{2}$ per cent alcohol and $\frac{5}{8}$ per cent acetic acid, however, yielded a better response than either alone at the optimum concentration. Recently, Brown (1928) has shown that the odor of the yeast upon which the larvae of the flies feed also serves to attract the flies in addition to the "odors usually associated with that yeast."

A striking case of insect attraction by odor was reported by Howlett (1912) for fruit flies belonging to several species of the genus *Dacus*. It was first found that oil of citronella exercised a powerful attraction for the males of these flies, the reaction being entirely confined to this sex. Further experiments (Howlett, 1915) showed that the attraction was due to the presence of methyl-eugenol in the oil of citronella. Experiments were, therefore, carried out with 1) eugenol, 2) iso-eugenol, 3) methyl-eugenol, and 4) benzo-eugenol. The first and fourth attracted no flies. The second, iso-eugenol, attracted the males of *D. diversus* very strongly and the males of *D. ferrugineus* to a slight extent. The third, methyl-eugenol, attracted the males of *D. zonatus* very strongly, and the males of *D. ferrugineus* to a considerable extent. The significance of these odor responses, however, was not clear, for Howlett was unable to connect them with sex attraction or food smells in any satisfactory manner. I have been unable to locate any subsequent papers of this author on this subject.

The most important systematic study of the physiology of olfaction in insects is the work of v. Frisch (1919) on the honey bee. Only a few of the results of this extensive and important work can be summarized here. Using methods similar to those previously described for this author, v. Frisch tested a series of 47 ethereal oils, and found that bees previously trained to the odor of one of these oils, namely, an essence of orange, singled out this odor with great certainty from most of the others. Four of the odors, however, were confused to a very considerable extent with the essence of orange. These four oils were all extracted in the same manner as the essence of orange from other species of citrus fruits, and all had in common, oil of lemon and linalool. Furthermore, to the human olfactory organ, these four odors were found to be more nearly like the essence of orange than any of the other odors employed. Further experiments showed, however, that the four odors in question were not completely alike to the bee, but only similar. The two odors most nearly alike, which can be distinguished by man only after considerable practice, also required long training for the bee to discriminate. Von Frisch concluded, therefore, that in these respects, the sense of smell in the honey bee was no more delicate than that of man.

THE OLFACTORY THRESHOLD

In addition to experiments permitting a comparison of the olfactory powers of the bee and man qualitatively, experiments were performed which allowed a quantitative comparison. The threshold concentration to which bees could be trained was determined for three odors: paraffin oil scented with the odor of tuberoses, bromstyrene, and methylheptenone. It was found in each case to be essentially the same or at least of the same magnitude as the threshold in man. These results on the bee differ from those on certain other forms. The males of certain moths are attracted to the females almost if not entirely by odor, and experiments indicate extraordinary olfactory acuity on the part of the males in perceiving this odor. Riley (1894) reports a case in which a male of *Philosamia cynthia* found its way to a female over a distance of one and a half miles. Unfortunately the conditions of the experiment, such as wind direction, etc., are not recorded. The results of Fabre's (1879–1904) classic experiments with other moths indicate a similar development of the olfactory sense. A single female of *Bombyx quercus*, of which this veteran naturalist had not seen a single example in twenty years of collecting in his locality, attracted no less than sixty males.

When we consider the size of the scent producing gland in the body of the female moth, and the volume of air in which the volatile product of this gland is diluted, it seems almost incredible that there can be a material concentration strong enough to stimulate. It is little wonder, therefore, that some zoologists have been tempted to believe in a non-material form of emanation, such as waves. But the ability of such waves to pass through simple air-tight containers in which the females are enclosed, indicates that we are dealing with a chemical stimulus. Like the mammals, therefore, the insects differ greatly in their olfactory powers, and man and the dog find their counterparts in the bee and the moth.

The olfactory sense of these lepidopterous males is not only quantitatively, but also qualitatively acute. Both Mayer and Fabre report that other strong odors are ineffective in making the odor of the female less discernible or less attractive to the male. Experiments carried out by v. Frisch with odor mixtures showed that bees also had, to a considerable extent, the ability to detect a small amount of the training odor in an odor mixture. In this respect the bees were found to exceed the average man in olfactory discrimination, but whether their olfactory powers would also exceed those of a man trained in olfactory discrimination, such as a perfume expert, is not certain.

Numerous experiments were carried out by v. Frisch with pairs of substances, similar in odor, with highly interesting results. In man two substances of different chemical composition may smell much alike, and two substances of similar chemical composition may smell differently. The same is true for bees. Each pair of substances tested, in which the two members, despite dissimilarity of chemical composition, smelled similar to man, appeared also to have a certain similarity for the bee. The significance of the results obtained with the bee is obvious, as v. Frisch points out, viz., that there is much more common to the physiological bases of smell in man and in the insect than would be expected from such differently organized sense organs.

THE SENSE OF TASTE

Until the last few years, the sense of taste in insects has received relatively little attention. The work of Will (1885) and of Forel (1908) constitute most of the older experimental work. Their experiments consisted in offering bees, wasps, and ants sugar or honey, and then substituting the same adulterated with various substances which are salt or bitter to the human tongue, or which are poisonous. The acceptance or refusal was then observed, and in this way certain facts were learned with respect to the gustatory powers of the insect.

More recently this problem has been attacked by more refined methods, which promise much more accurate and critical results. As I have shown (Minnich, 1921), it is possible to investigate many aspects of the chemical senses of insects by choosing species with extensible mouth-parts, and by using the extension of the proboscis as an indication of chemical stimulation. Suitable animals for this purpose are certain of the large flesh flies, such as various species of *Calliphora* and *Phormia*. These insects can be mounted individually with a bit of wax on a wire handle, and thus readily manipulated. If fed twice a day on a 1M saccharose solution they may be kept alive and vigorous for a period of several weeks or more. If the flies are kept in a condition of satiety with respect to water, the effect of various other solutions upon the proboscis extension may be observed. Thus, if a minute brush saturated with distilled water is gently applied to the oral sucker of such an animal, there is no response; but if a similar brush saturated with a 1M saccharose solution is applied, violent extensions of the proboscis result (Minnich, 1926b). Clearly the sense organs of the oral sucker are able to discriminate between pure water and an aqueous solution of saccharose. A study of responses to other substances is now under way in my laboratory.

Using these methods, it is also possible, with care, to stimulate certain of the hairs of the oral sucker individually. The margins of the aboral surface of the oral sucker are clothed with hairs, the outermost of which are long and curved. Under appropriate conditions, the application of 1M saccharose to a single one of these hairs may effect a proboscis extension, whereas the application of water will not. Hence these hairs are gustatory in function. Insofar as I am aware, this is the first case in which it has been possible to identify positively, by local stimulation, a chemoreceptor in an insect, the nearest approach to it being the work of v. Frisch in connection with the pore plates of the antennae.

THE THRESHOLD FOR TASTE

Recently v. Frisch (1927) has published some highly interesting results of experiments on the sense of taste in the honey bee. After training bees to feed on sugar water at an experimental table, he substituted various concentrations of different sugar solutions, or sugar solutions adulterated with other substances, and observed whether the bees accepted or rejected the substitute. Unfortunately, this method fails, as v. Frisch points out, to measure the real degree of sensitivity of the animal in many cases. Thus an animal may refuse to drink sugar water of a given concentration, and yet be able to distinguish it from water. For saccharose solution the threshold was between M/4 and M/8, or about eight times more concentrated than the human threshold. Check experiments showed that the perception of the sugar solution was not due to smell nor to such physical properties as viscosity and osmotic pressure. Hence it was tasted in the real sense of the word. A wide difference was found between the bee and man with respect to other substances which are sweet to the human taste. Thus while fructose tastes twice as sweet as glucose to us, it tastes less sweet to the bee. Lactose, moreover, appears to be completely tasteless to the bee. Other substances which are sweet to us, such as the sugars galactose, rhamnose, arabinose, the alcohols mannite, sorbite, and dulcite, and such substances as saccharin and dulcin, appear to be almost or wholly tasteless to the bee. In no case are they sweet.

To test the sensitivity to acids, various concentrations of hydrochloric and acetic acids were mixed with 1M saccharose, and the concentration noted which was sufficient to cause great hesitation in the acceptance of the solution. For hydrochloric acid this was *n*/80, the pH of the solution being 1.9; for acetic, *n*/5, the pH of the solution being 2.7. Just as in man, therefore, the acetic has a greater effect than would be expected on the basis of the hydrogen ion concentration alone.

Experiments with sodium chloride showed that a concentration of *n*/2 in 1M saccharose solution was refused by the great majority, while a concentration of *n*/8 was accepted by all. Suspecting that although *n*/8 was taken, it was still perceived, v. Frisch devised a very clever means of testing the matter. A known amount of solution was put out, and a careful record kept of the number of visits required for the bees to remove it. From these data the average crop load was computed. For 1M saccharose containing either *n*/8 or *n*/16 NaCl this was less than for pure 1M saccharose. For 1M saccharose containing *n*/32 NaCl, it was the same. Thus, although the bees accept 1M saccharose, adulterated with NaCl up to *n*/4 NaCl, they are able to distinguish the NaCl in dilutions as great as *n*/16. Experiments on the sensitivity of the human tongue to these mixtures showed that the threshold for NaCl under the same conditions was about the same in man as in the bees.

With the bitter substances, however, the threshold of the bee was found to be much higher than in man. A 1M saccharose solution containing M/2000 quinine hydrochloride, which is strongly bitter to us, was accepted by all bees, while a similar solution containing M/500 quinine, which is horribly bitter to us, was drunk by many. Indeed it was not until the quinine reached a concentration of M/300 that the mixture was generally refused. Thus, while exhibiting many points of similarity with the sense of taste in man, the sense of taste in the honey bee also shows some striking differences.

TARSAL ORGANS OF TASTE

But the sense of taste in insects is not confined to the mouthparts. As I have been able to show (Minnich, 1921, 1922a, 1922b, 1926a) for certain butterflies and flies, it is also present in the tarsi. Indeed, scattered observations seem to indicate that the tarsal organs of taste are of general occurrence among the arthropods. If a mourning cloak butterfly be observed as it approaches a bit of decaying apple, it may frequently be seen to extend its proboscis the moment one foot makes contact with the apple. That the organs concerned are gustatory and not olfactory may be demonstrated by a simple experiment. If, under appropriate conditions, a red admiral butterfly, *Pyrameis atalanta*, is placed in a holder which grasps the two wings and allows the feet to rest on a small platform of wire screen, and a needle bearing a small cotton swab soaked in apple juice is held 1 mm. from the ventral surface of any one of the tarsi, there is no response. The moment the swab is allowed to touch the tarsus, however, the proboscis is immediately extended.

In *Pyrameis*, studies were made of the effects of various dietary conditions, such as total inanition, water diet, and 1M saccharose diet, on the responsiveness to water, to 1M saccharose, to M/10 quinine hydrochloride, and to 2M NaCl. It was found that the response to water was capable of absolute control. With the administration of sufficient water, the response fell to zero, and remained there as long as water was given the animal in sufficient quantity. If the animal were subjected to total inanition, however, the response to water rose more or less gradually to 100 per cent, where it remained until water was administered, or until the animal died. The response to 1M saccharose, on the contrary, could not be controlled by feeding 1M saccharose. No matter how much of this solution was given the animal, it still responded regularly to it. The curves of response to NaCl and quinine varied with the time and with the animal from 0 per cent to 100 per cent. In general they followed neither the curve of water response, nor the curve of sugar response, nor the changing dietary conditions, nor each other. The curves of response to water, to 1M saccharose, to 2M NaCl, and to M/10 quinine hydrochloride were thus quite independent of each other. From these facts, it seems fair to conclude that these three solutions are distinguished from each other and from water by the tarsal organs of taste.

Experiments with varying dilutions of saccharose were also made during these different dietary periods to ascertain whether there was any variation in the threshold of the response. The results showed that there was such a variation. During periods of total inanition followed by periods of water diet, the threshold of response to saccharose gradually fell. With the initiation of a new period of saccharose diet, it rose abruptly to a level of not over M/10, where it remained approximately constant throughout the period. The interesting and surprising thing about these experiments was the extent to which the threshold fell during periods of prolonged inanition with respect to saccharose. It was found that saccharose concentrations of M/3200, M/6400, or even M/12,800, in some cases, could be distinguished from distilled water by the animals. The tarsal sensitivity of *Pyrameis* to saccharose may thus be at times as much as 256 times that of the human tongue.

As our knowledge of the chemical senses of insects has increased, a more accurate comparison has become possible with the corresponding senses of the vertebrates, including man. One striking outcome of this comparison is the discovery of many rather fundamental similarities. Between the chemical senses of insects and man, however, there appears to be one outstanding difference, and that is the greater acuity of these senses in many insects. Whether increased knowledge will further verify this distinction cannot, of course, be predicted. But that insects should be capable of exceedingly fine discriminations of this nature is to be expected, inasmuch as they are a group of organisms in which the chemical senses have come to play the dominant rôle in general behavior.

This paper was presented in part at the 1927 meeting of The Entomological Society of America at the Symposium on the Physiology of Insects.

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DEATH FROM LOW TEMPERATURE AND RESISTANCE OF PLANTS TO COLD

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IN THE last few decades, as is well known, the problems of death from cold and winter hardiness have attracted much attention in modern plant industry. This has especially been the case since the origin of new varieties by plant breeding and the introduction of new varieties from foreign countries got in full swing. It, therefore, seems appropriate that, when a review of all problems of this kind appeared, it should come from the hand of a plant breeder. Recently Doctor A. Åkerman of the Svalöf Plant Breeding Station in Sweden has published a detailed report of more than ten years work along this line and at the same time has given a thorough and critical review of all questions concerned (2). It is at present, no doubt, the best and most encyclopaedic treatise on the topic available. On the basis of this book I shall give below a short statement of the present day status of this field of the biological sciences.

THE MECHANISM OF CELL DEATH FROM COLD

The first question that presents itself when one is dealing with these topics, is of course: What are the causes of death from cold? Many workers have dealt with this matter and many are the conclusions that have been drawn. As yet it does not seem possible to form a definite conception of the immediate causes of death from cold, arising from too abundant ice formation in the cells. Besides the ice formation low temperature in itself is able to provoke injuries. Every organism has a fixed minimum temperature, below which it cannot live for long, and in some plants this minimum temperature is considerably higher than 0°C. (9). At certain temperatures even the speed with which the tissue thaws out may be of importance (1). If the temperature, however, is below that point where the cells freeze to death then, of course, the speed of thawing out is of no consequence. In plant tissues the ice appears at first in the intercellular spaces. With continued cooling, as a consequence of the low vapor pressure when ice is present, either water must be extracted from the cells or ice formation must occur in them (16). The latter case is only possible when the temperature has fallen below the freezing point of the cell content. If the cell content, however, is undercooled then its vapor pressure may be higher than that of the ice. In this case water again will move out through the cell walls to the ice crystals in the intercellular spaces. This desiccation by freezing temperatures can be detrimental and kill the tissue; it is, however, not only the loss of water in itself but also, among other things, its mechanically coagulating influence on the plasmic colloids that is of importance (8).

Two main groups of factors play an especially important part in determining the association between resistance to cold and other physiologic conditions in the plant cell. These are (1) the possibility of undercooling, and (2) the water-retaining power of the cell content and the resistance to ice formation thus originated. An association between the possibilities of undercooling and the cell size has been demonstrated in that tissues with small cells will be more readily undercooled, whereas tissues with large cells will freeze suddenly on the slightest shaking at or below the freezing point (18). The resistance of the cell content to ice formation depends partly upon the osmotic properties of the constituents dissolved in the cell sap (6) or, eventually, in the protoplasm, and partly upon the capacity for swelling of the plasmic proteins and other colloids (10, 11). With falling temperature the latter seems to grow as a result of an increase of the quantity of certain comparatively simple organic substances, such as hexoses and pentosans (2, 12, 14, 15). Disregarding these relatively simple conditions, one must also take into account a whole complex of other factors and circumstances that influence the resistance of the cell or the tissue to cold, e.g. the specific organization of the protoplasm and its chemical composition.

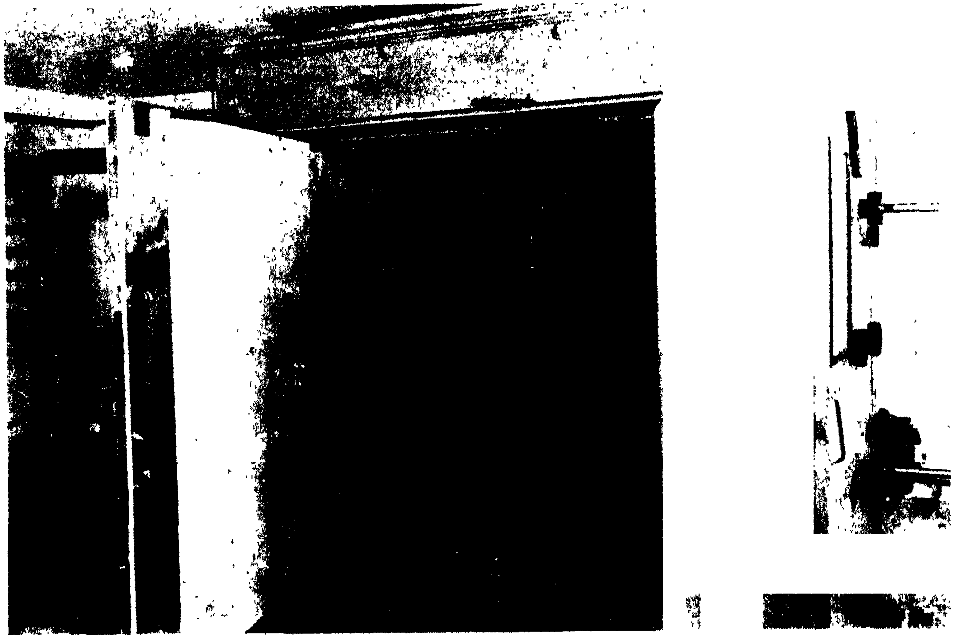

FIG. 1. THE REFRIGERATOR AT SVALÖF WHERE SMALL WHEAT PLANTS ARE EXPOSED TO LOW TEMPERATURE IN ORDER TO MEASURE THEIR RESISTANCE TO COLD

It is of great importance that in different varieties of many plant species a certain correlation can be demonstrated between resistance to cold and other easily determinable factors, such as the osmotic value of the cell content at the point of incipient plasmolysis (2, 4, 6, 13), the percentage of reducing sugars (2, 12, 13), and coagulable nitrogenous constituents (12), and the quantity of dry matter (3, 5, 12, 17). So in some plant species it is possible to get an idea of the winter hardiness by investigating these factors. E.g. in wheat it is appropriate to analyse the quantity of dry matter, the osmotic pressure at incipient plasmolysis, the capacity of reducing Fehling's solution, and the resistance against expression of sap from the tissues by mechanical pressure (12). The direct refrigerator experiments might, however, be the most practical and reliable method for supplementing the observations in the field, whereas the other methods should be used more as a control and supplement to the first mentioned.

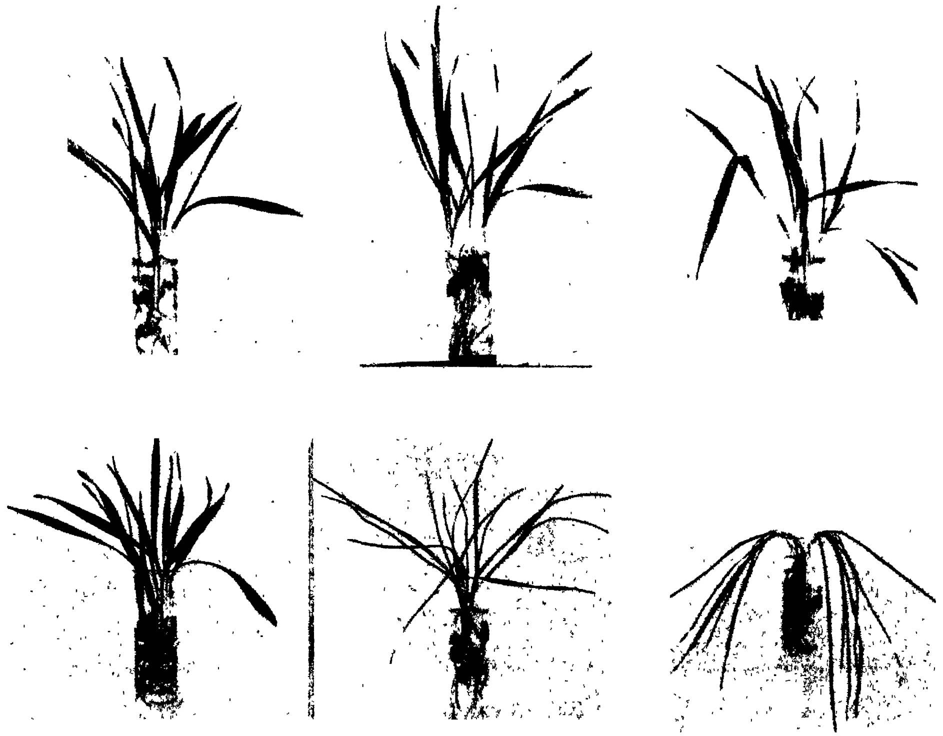

Fig. 2. Plants of (from left to right) Swedish Velvet and Danish Small Winter Wheat and Halland Spring Wheat; Before (upper row) and After (lower row) 3 Hours Freezing to −14.5°C.

THE PREDICTION OF HARDINESS

As to the winter hardiness of different wheat varieties, it is evident that the possibility of its exact graduation in different ways must be of great importance to the plant breeder. For example, when working with crosses between rather hardy varieties, which one expects to be seriously injured by the winter cold only once in three or four years, it must be very valuable to be enabled by other means to select every year for winter hardiness. Such means are refrigerating experiments and investigations of the above mentioned properties, correlated with cold resistance. The first thing to be considered must be what winter hardiness is and which different factors it depends upon. By a thorough and critical examination of the results of a great number of trials both at Svalöf and at the branch stations of the Swedish Seed Association, Åkerman (2) concludes that in Sweden resistance to cold is the most important factor determining the differences of varieties in winter hardiness. Many other factors may partly account for winter hardiness, but towards these the investigated varieties all react in about the same way. Among such factors might be mentioned heaving, desiccation, damage caused by ice formation in the field, the vigor of the seed, and the stage of plant development depending upon it. The degree of winter hardiness of wheat might thus be well determined by means of refrigerator experiments. Åkerman has made a large number of such experiments by different methods in his refrigerator establishment at Svalöf designed for this purpose. It appeared that the most scrupulous selection and treatment of the plant material is needed for bringing out reliable differences as to resistance to cold of the individual varieties. The plants must all be of the same age and at the same stage of development. They must have grown under normal conditions in the field and must have been exposed to low temperature some time before they are refrigerated. Taking these precautions it is, however, possible by graduating the damage from cold of the frozen and again thawed out plants to get very close agreement as to the degree of winter hardiness with the results of the field trials and with practice. Åkerman has been able on the basis of the refrigerator experiments to classify his wheat variety material in ten different hardiness groups and in these groups he can also to a certain extent range the individual varieties. The order of varieties so obtained agrees strikingly well with many years observations of the field trials.

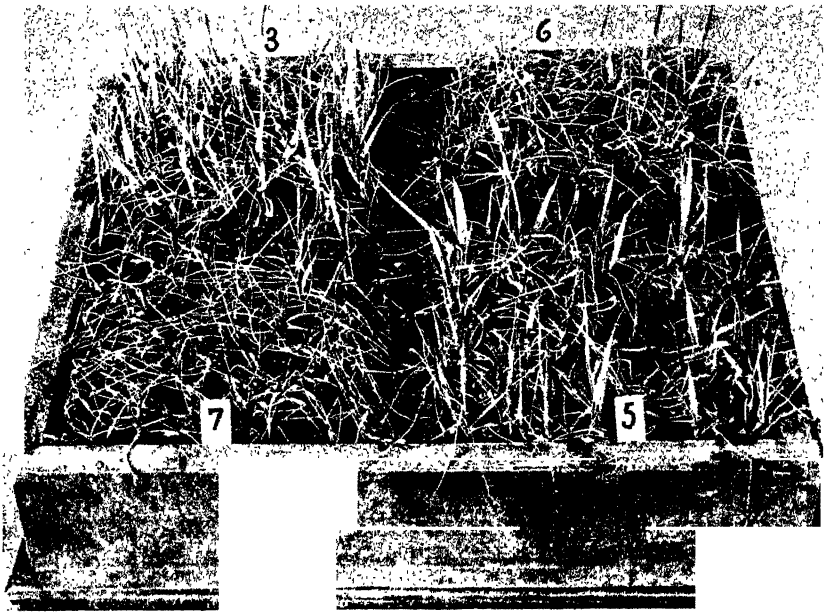

Fig. 3. Flat with Four Wheat Varieties Frozen to −12°C.
Nos. 3 and 5 hardly injured, most plants still living. No. 7 strongly injured, only a few plants living.

The determination of factors associated with resistance to cold has also been very successful. In co-operation with different chemists, particularly J. Lindberg, Åkerman (2) has investigated the reducing capacity (sugar content) of leaves of individual cold resistant wheat varieties. In all varieties as yet examined an apparent correlation between reducing capacity and resistance to cold (winter hardiness) has been established, at least during the period of dormancy in winter. The samples should be taken at low temperature when the state of the weather is stable. In periods of highly variable weather changes in resistance to cold and sugar content appear that will give a conception of the variety differences quite different from the normal one. This is even the case in spring time when the plants start growing. Using three different methods: field trials, refrigerator experiments, and sugar analysis, good agreement between the different methods was obtained and, in the case of progenies from crosses, very reliable segregations as to low and as to high resistance to cold have been established. Even transgressive segregations could be shown in some cross progenies. As might be expected, the osmotic pressure of the cells in a state of incipient plasmolysis is closely associated with the reducing power (sugar content) of the wheat leaves and so can be used as a measure of resistance to cold.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that The Quarterly Review of Biology *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* The Quarterly Review of Biology, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

ADDITIONS TO THE PALAEONTOLOGY OF THE PACIFIC COAST AND GREAT BASIN REGIONS OF NORTH AMERICA. *Contributions to Palaeontology from the Carnegie Institution of Washington. Publication 346.*
By Remington Kellogg, John C. Merriam, Chester Stock, Ralph W. Chaney, and H. L. Mason.
Carnegie Institution of Washington
$3.00 *Washington, D. C.*
6⅞ x 10; 158 (paper)

In this volume are included five studies:

I. *Study of the Skull of a Fossil Sperm-Whale from the Temblor Miocene of Southern California*, by Remington Kellogg. The author describes in great detail the fossil bones of an adult sperm whale and compares with this a partially preserved specimen of a young sperm whale of the same period and region. Nine plates give illustrations of both specimens.

II. *Fossil Pinnipeds from California*, by Remington Kellogg. In this paper are described the portions of the skull of a fossil pinniped, belonging to the group known as eared seals; also, portions of limb bones of two other species of fossil seals, probably of an undescribed form. There are eight figures illustrating the fragments described.

III. *A Hyaenarctid Bear from the Later Tertiary of the John Day Basin of Oregon*, by John C. Merriam and Chester Stock. This paper deals with several hyaenarctid teeth and fragments collected in 1925. The material proved to be some of the missing parts of a bear found in the same locality in 1925. Illustrations of the material are given.

IV. *Geology and Palaeontology of the Crooked River Basin, with Special Reference to the Bridge Creek Flora*, by Ralph W. Chaney. *With a chapter on the Tertiary Insects*, by T. D. A. Cockerell. The first part of this paper deals especially with a study of Tertiary floras of Eastern Oregon. Observations on the general geologic features made in connection with the work and a brief account of the vertebrate and invertebrate fossils found are included. The flora is extensively treated both quantitatively and qualitatively and local distributions are given. Twenty plates serve to illustrate the paper as well as to arouse in the reader a longing for the opportunity to go hunting fossils in the Crooked River Basin.

V. *Fossil Records of Some West American Conifers*, by Herbert L. Mason. The fossil species of conifers are described in detail and the distribution of these, so far as known. A comparison is made with the present day distribution of conifers.

CREATION BY EVOLUTION. *A Consensus of Present-Day Knowledge as Set Forth by Leading Authorities in Non-Technical Language that All May Understand.*

Edited by Frances Mason.

The Macmillan Co.
$5.00 5¾ x 8⅝; xx + 392 *New York*

A beautifully printed collection of essays by twenty-six English and American scientists, written, according to the Editor, "to render help to those who seek knowledge of the nature and bearings of the great fact of Evolution." There is a "Foreword" by Henry Fairfield Osborn, and an "Introduction" by Sir Charles Scott Sherrington. A group of selected references is appended to almost all of the articles. These in turn are usually followed by quotations from the writings of scientists or of otherwise famous men pertaining to the subject under discussion.

Each contributor discusses, in non-technical language, the meaning of evolution from the viewpoint of his own particular subject. It is at once apparent from a glance at the names of the distinguished men who have contributed that the book can justly claim authoritativeness of the highest order. Furthermore the writing is generally extremely well done, from a literary viewpoint.

For the professional biological reader, however, this book contains little that is new. For the general reader curious about the universe, it will furnish sound and interesting reading, much of which will certainly be novel. As for the fundamentalist, at whom this book was specifically aimed, we suspect, he can read these essays not only without having his faith in the Creator in any way shaken, but in the marvelous processes of Nature here disclosed he will be disposed to find a further and welcome confirmation of his belief in the far-sightedness and omnipotent skill of *Jahveh*. So it should, like Prohibition, leave everybody happy.

EVOLUTION AND WAR.

By Reginald Cock. *Elliot Stock*
3 s. 6 d. 4⅞ x 7¼; 111 *London*

This is a new edition of the author's *Genesis v. Evolution*, reviewed here, along with his portrait, in March, 1927. The present work contains some scattered additions, and two new chapters, one on Civilization and one on War. The author is not one of the more formidable of Fundamental logicians, as the following sample will indicate:

> How comes it that Moses made no mistake? We can answer, only by inspiration; no human being witnessed creation, so an account of it, to be true, must be inspired by God. And it is reasonable to suppose that God Who gave man language, and the power to read and write, communicated to man those things which were necessary to his understanding and happiness.
>
> I quite agree with Sir Arthur Keith that it would be difficult for any modern teacher of medical students to assure his class, even in allegory, that the first woman was a modified rib. Following our Authorized Version we are in the habit of saying that Eve was one of Adam's ribs. But, as Lenormant says, the word *çêlâ* elsewhere means "side," and not rib.

We suppose that that makes it quite simple for a Christian.

WILD BIRDS INTRODUCED OR TRANSPLANTED IN NORTH AMERICA. *U. S. Department of Agriculture Technical Bulletin No. 61.*

By John C. Phillips.

Government Printing Office
10 cents *Washington, D. C.*
$5\frac{7}{8}$ x $9\frac{1}{8}$; 63 (paper)

A list of the different species of birds whose introduction into North America has been tried, with accounts of the attempts. The material is of particular interest to the thoughtful student of evolution.

GENETICS

TWINS AND ORPHANS. *The Inheritance of Intelligence.*

By Alex. H. Wingfield.

J. M. Dent and Sons, Ltd.
10 s. 6 d. $5\frac{1}{2}$ x 8; 127 *London*

This book, which is a thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy in the University of Toronto, is an attempt to measure the relative importance of heredity and environment in determining general intelligence, intelligence being defined as the mental function measured by intelligence tests. The author's methods seem to us of somewhat dubious validity, especially in his treatment of his orphan population. He first states:

> If the cause, or partial cause, of the similarity found between twins or siblings is due to similarity of environment and training, we should expect to find that children who have been reared for a considerable period of their earlier lives, especially during the "plastic" period of early childhood, in a very nearly constant environment would show a fair degree of resemblance in various mental traits when paired with each other at random. In order to verify or disprove this hypothesis, the same tests that were given to the twins, as reported in the preceding portion of this study, were given to a group of orphan children who had been reared together for 25 to 75 per cent of their lives.

He then goes on to say: "Two methods of pairing the orphans were used. The first method was to pair an orphan with another who was nearest to him in chronological age. The second method was to pair the orphans with each other at random."

His findings as a result of this procedure are that "not only is there no resemblance when orphans are paired at random for intellectual traits, but there is a fair degree of inverse correlation. When the orphans are paired to the nearest age, we note in Table XXII that there is a slight degree of resemblance in the case of the I.Q.'s and arithmetic scores, while in the A.Q.'s and spelling scores there is a somewhat more marked correlation, although it is still low."

What we should like to know is what else he expected to get? If he took any population whatever, measured any character whatever, paired individuals at random, and determined the correlation coefficient, what value would he expect?

WILLIAM BATESON, F.R.S., NATURALIST. *His Essays and Addresses, together with a Short Account of his Life.*

By Beatrice Bateson. *The Macmillan Co.*
\$8.40 $5\frac{3}{8}$ x $8\frac{3}{4}$; ix + 473 *New York*

This volume includes a memoir of Bateson by his wife, followed by a selection of his papers. The memoir is excellent reading, and gives a very attractive picture of Bateson's personality. It is somewhat lacking on the purely scientific side; we should like to see it supplemented by a fuller account of the development of Bateson's scientific ideas. Some of the papers will no doubt be familiar to professional geneticists; but they can be recommended generally. They include not only papers specifically on heredity, but also papers on more general topics; in these we find much sound common sense, though we do find him saying that, "Prohibition, if it is maintained, will rank among the great disasters which from time to time have checked human progress." This, however, was written in 1919, and shows that he probably overlooked the ingenuity of Americans in developing adequate sources of supply to replace those cut off.

* * *

L'IMMUNITÉ DU NOURRISSON. *Contribution à l'Étude de l'Immunité Héréditaire.*
By Germaine Dreyfus-Sée. *Louis Arnette*
20 francs 6½ x 10; 194 (paper) *Paris*

The first part of this treatise is concerned with a review of what is known regarding congenital passive immunity, and its transmission from mother to child through the placenta, and through the milk. The second part deals with the tissue immunity of the baby. The author concludes that the infantile organism develops agglutinins very little if at all and has in general but feeble anti-microbic defense mechanism in the serum. It has, on the other hand, a remarkable resistance to toxic substances—drugs and the like. The third part of the book discusses true hereditary immunity, and contains an account of some interesting experiments with mice, in which two strains were bred differing widely in their resistance to pneumococcus infection. The book is a welcome addition to the literature regarding the genetic or constitutional factor in disease. There is an extensive bibliography.

* * *

VERHANDLUNGEN DES V. INTERNATIONALEN KONGRESSES FÜR VERERBUNGSWISSENSCHAFT BERLIN 1927. *Band I and II.*
Edited by Hans Nachtsheim.
Gebrüder Borntraeger
100 Marks for 2 volumes *Leipzig*
7¼ x 10⅛; viii + 784 (paper)
viii + 785–1646 (paper)

These stately volumes contain the complete records of what was perhaps the most successful and important International Genetics Congress ever held. All the arrangements were extremely well managed. The volumes were promptly published and excellently edited. It is impossible to take the space here even to list the notable series of papers in all fields of genetics which were read at the Congress, and are here published in full. The Americans were well represented, both in respect of numbers and of the quality of the papers presented.

* * *

THE BOOK OF DOGS. *An Intimate Study of Mankind's Best Friend.*
By Ernest H. Baynes.
National Geographic Society
$2.00 6⅝ x 9⅝; 109 *Washington*

This volume describes and figures the principal breeds of dogs. It is beautifully illustrated. There are color portraits of 76 types from paintings by Louis Agassiz Fuertes and Hashime Murayama.

* * *

MUTATIONSTHEORIE DER GESCHWULST-ENTSTEHUNG. *Übergang von Körperzellen in Geschwulstzellen durch Gen-Änderung.*
By K. H. Bauer. *Julius Springer*
3.90 marks *Berlin*
5¾ x 8¾; 72 (paper)

A well-written and interesting little brochure developing the theory that cancer arises as a somatic mutation, that is, a genic change in the chromosomes of a somatic cell. The author's main basis biologically is found in Boveri's classic memoir on the cytology of malignant cells, which by the way, is shortly to appear in English translation. Dr. Bauer is an associate professor of surgery at Göttingen and knows the clinical side well. Both medical men and biologists will find much that is suggestive in his theory.

HOW WE INHERIT.

By Edgar Altenburg.
Henry Holt and Company
$3.00 5⅜ x 8½; vii + 273 *New York*

A very readable little essay touching the principles of genetics sufficiently lightly to keep it unmarred for the reader who has "no previous knowledge of biology."

GENERAL BIOLOGY

PHYSIOLOGY AND BIOCHEMISTRY OF BACTERIA. *Vol. I—Growth Phases; Composition, and Biophysical Chemistry of Bacteria and their Environment; and Energetics.*

By R. E. Buchanan and Ellis I. Fulmer.
The Williams & Wilkins Co.
$7.50 6 x 9; xi + 516 *Baltimore*

This extensive work, only one volume of which is completed at present, has been planned with the view of placing in the hands of those especially interested in the subject, a compilation and systematization of material relating to the physiology of microörganisms, particularly of the bacteria, yeasts and molds. Much careful work has gone into the preparation of Volume I, which serves chiefly as an introduction and an outline of the subject. By this arrangement there is made apparent to the investigator many of the untouched fields of the physiology of microörganisms which are yet to be explored.

The book is well indexed, has 78 illustrations and a bibliography of several hundred titles. It will be particularly valuable to the general biologist. Bacteriology has become so specialized to particular ends that we all tend to forget that after all it is a branch of general biology. This treatise of Buchanan's and Fulmer's will serve well the extremely valuable purpose of making once more a closer *liaison* with the parent subject.

LA VIE, LA MALADIE ET LA MORT. *Phénomènes Colloidaux.*

By Auguste Lumière. *Masson et Cie*
45 francs *Paris*
5⅜ x 8¾; xxiii + 520 (paper)

This volume is a continuation of the author's well known writings on the biological significance of colloids. It supports and further develops his thesis that the colloidal state is a necessary condition of life, and that the destruction of this state, that is to say the flocculation of the colloids, causes sickness and death. A short first part gives an elementary account of the properties of colloids. The second part, also short, discusses life in its relation to the properties and normal evolution of colloids, with particular reference to the phenomena of growth and senescence. The third and fourth parts, which make up the remaining two-thirds or more of this book, are concerned with pathological phenomena, especially in relation to the flocculation of colloids in the fluids and cells of the body. The book is well written and illustrated. While its chief interest is special to the pathologist, the general biologist will find it worth reading.

THE CORAL REEF PROBLEM.

By William M. Davis.
American Geographical Society
$6.00 (to libraries $5.00) *New York*
6¾ x 10; 596

In this extensive research the author, who considers coral reefs, especially in their barrier and atoll forms, as among the most extraordinary of natural structures, has brought forth new evidence to support the theory of coral reef formation outlined many years ago by Darwin. He states that "as new facts have been brought to light, it has been most impressive to note the ease with which they have been explained by inevitable extensions of the old theory." He finds only one serious exception, namely the islands of the marginal belts of the coral seas. Here, "Darwin's theory must be supplemented by the wholly new process of low-level abrasion, first brought into the problem in recent years by Daly." Various other theories of coral reef formation are presented and discussed in detail.

There are numerous illustrations and diagrams throughout the text. A bibliography of several hundred titles and an excellent index complete the volume.

CILIARY MOVEMENT.

By J. Gray. *The Macmillan Co.*
$4.25 5⅜ x 8¾; viii + 162 *New York*

This volume is a study of ciliary movement from the physiological point of view. About half the book is devoted to a study of the mechanics of ciliary movements, including both the actual movement of the cilium itself and the work done by the cilium on the surrounding medium. There follow chapters on the relation of ciliary movement to ionic equilibria, on the metabolism of ciliated cells, on metachronal rhythm and ciliary control, with a final chapter on the distribution and functions of cilia in the animal kingdom. The book gives an excellent summary of our present knowledge, and a good indication of the directions in which further study is needed. There is a good bibliography and an index.

KAUSALITÄT UND VITALISMUS VOM STANDPUNKT DER DENKÖKONOMIE.

By Hans Winterstein. *Julius Springer*
4.80 RM. 6¼ x 9⅝; 51 (paper) *Berlin*

The second edition of an attack upon vitalistic philosophies and modes of thinking, by a distinguished experimental physiologist. He declares that his (and others') insistence on the necessity for physico-chemical explanations of the phenomena observed in living things is no dogma, as the vitalists insist it is, but is simply a necessary consequence and integral part of the very essence of explanation itself. We are unable to see that Winterstein contributes anything essential to this metaphysical discussion which has not already been said before, at least as well.

HUNTING UNDER THE MICROSCOPE.

By Sir Arthur E. Shipley.
The Macmillan Co.
$2.50 4¾ x 7¼; 184 *New York*

This is a well-written little book, whose purpose is to encourage mucking about in ponds and ditches, and examination under the microscope of the results, by amateur nature-lovers. It is very much the sort of book to give to a bright boy who has access to a microscope. We suspect that it would teach him vastly more than a good many school courses.

HUMAN BIOLOGY

HEALTH AND WEALTH. *A Survey of the Economics of World Health.*

By Louis I. Dublin. *Harper and Brothers*
\$3.00 $5\frac{1}{4}$ x $8\frac{1}{8}$; xiv + 361 *New York*

The energetic statistician of the Metropolitan Life Insurance Company who is the author of this volume has earned the admiration of everyone interested in the advance of human biology. In exploring the records of his company for light on questions concerning broad biologic aspects of human pathology he has been a pioneer, and his recent writings with Lotka are fundamental for the theory of vital statistics. The present work is a collection of fifteen essays, selected from addresses, and is directed to the general reader. The topics are varied in character: the first three deal with the economic aspects of disease, the next three with heart disease, cancer and tuberculosis as they affect the general population, and the rest with various phases of vital statistics that are of immediate social interest, prohibition being one. All of them are clearly and interestingly written.

A zealousness on behalf of the public welfare runs through the work as its *Leitmotiv*. The author is everywhere ardent in advocating increased public activity for the sake of its own health. To no small degree this diminishes the objectivity of his studies, and lowers their critical scientific value. We would frankly apply this criticism throughout, but there is not space here for an elaborate analysis and the most we can do is to give several illustrations of our meaning.

On page 18 we read

> Where life is long, debilitating sickness is less prevalent and economic production is highest. The extraordinary prosperity which has been witnessed in the United States is, in large measure, the result of the control which has been exercised over disease; of the freedom which men and women have attained to labor without interruption and without fear; the opportunity that our children have gained to grow up in the care of father and mother, amply supplied with the necessities of life and preserved from the trials and sorrows of broken families. Where, as in India, the duration of life is short, existence is surrounded by fear of death, and of crippling, and of invalidism.

We submit that there is a possible confusion of cause and effect here.

In Chapter V, the author essays to determine the cause of the decline of the tuberculosis death rate. He sees two possible explanations, the first, that it is due directly to the deliberate modification of the environment by man.

> With that thought in mind, the proponents of this view early developed a broad campaign of general education of the population. A knowledge of personal hygiene was widely disseminated in order that individuals might learn how to strengthen their resistance against the development of active symptoms of the disease. This was the keynote of the general campaign against tuberculosis as outlined by this Association when it was founded in 1904.
>
> The campaign against tuberculosis was accordingly directed toward finding the large numbers of individuals who were breaking down with the disease, to strengthen their resistance, and to make them well again if possible, and, second, to prevent their infecting others.

The other minimizes the importance of environmental factors. "Those who support this second view emphasize the all importance of the genetic—that is, the constitutional factors." Pearl and Pearson are quoted as typical proponents of the second view. Now we do not speak authoritatively for either of the quoted authors, but our impression is that their views and the issue are quite misstated here. The general question approached by them in different ways concerned a weighing of effectiveness as between the deliberate public health campaign against the disease, typified, for instance, in the above quotation from Dublin, and factors not associated with this direct attack. Inherited constitution is only one of these; others that come to mind as possible or even likely are decreased virulence of the bacillus, the gradual immunization of the community by small repeated infections, the improvement of physical condition incident to general betterment of economic status. Any considerable importance attached to such factors as these would as effectively weaken the case for large public expenditures for anti-tuberculosis campaigns as would the establishment of constitution as the significant determinant. But the author labors a long argument against the all sufficiency of the genetic explanation, and from his unfavorable result, makes the facile conclusion that the effectiveness of the public health attack on tuberculosis has been demonstrated.

Nor can we follow sympathetically, much as we admire the underlying work, the argument of Chapter IX on what the author calls the "true rate of natural increase." Here the point is made that the birth rate, and therefore any rate of increase derived from it, depends on the age distribution of the female population. The present population is artificially inflated, he says, in the child producing ages, a condition that will disappear as the population becomes stabilized. A rate of natural increase calculated for this stabilized population turns out to be 5½ instead of 11, which is the figure usually given. Now such a calculation assumes the constancy of existing age specific rates during the period required for stabilization. Lotka has estimated how long this should be, and if our memory is dependable it is something less than a century. For that length of time the death rates must remain stationary at their present value. Elsewhere, when the author is urging a different thesis, he estimates a 67 per cent decline of the tuberculosis rate in the next ten years! As a matter of fact the true rate of increase at any time is the quantity disparaged by the author, the existing death rate minus the birth rate; it is this figure that tells how many individuals are added to the population. To calculate for future decades what will be our rate of increase must include an estimate not only of what will be the future age distribution but also the future specific rates. Until such a calculation is made no such dire conclusion as the author's is justified.

> After correcting for the purely incidental feature of a peculiar temporary age distribution, our natural rate of increase was reduced to one-half of its crude figure. We find ourselves, therefore, with a rather narrow margin of safety dividing us from the downhill slopes of actual population decrease.

* * *

HUMAN VALUES AND VERITIES.

By Henry Osborn Taylor.

The Macmillan Co.
$2.75 6 x 9; xiv + 282 *New York*

An elderly gentleman, a jurist, an historian, a philosopher who has a deep attachment to science, here sets down his thoughts on life's meaning. The devil's question—is it in its totality worth the living?—he circumspectly avoids, but out of his individual experiences he essays to synthesize a body of evaluating principles. "There ought to be some rational process, set in general human knowledge and experience, by which standards of worth and truth suitable for thoughtful people might be established." Life's worth is found in two elements, values and validities. "What is of value to a man comes as an interwoven or organic response to a desire or activity of his own; in general, to his impulse to live and function. . . . . Indeed what is of human value seems identical with the very functioning itself of human faculty." Validity, which stands somewhat apart from value, has to do with the curiosity that impels man to objective truth. "Validity seems a realization within me of that which corresponds with fact, that is, with such reality as I may apprehend." The measure of these for the achievement of the good in life is to be found in their coördination in the whole being. "For the individual the final verdict upon the value of a given effort or the validity of a thought lies in the concert of his faculties—if such agreement can be found."

Provided with these criteria, the philosopher explores various departments of human faculty, history, science, philosophy, religion, practical affairs. In history, the author finds a changing of values and validities from age to age and from people to people. In the whole he sees progress. "I cannot survey the tale of history, with prehistory for prolegomena, without a conviction of human advance—only one must not think in decades or centuries, but in millenia or aeons." As between science and philosophy there is no real conflict; both are a response to thoughtfulness with a different psychological stress. "The philosopher is the thoughtful introvert, while the scientist is the rational observant extravert." And then again, in the chapter on Science proper, more grounds are found for a *rapprochement*. Philosophy is brought up to Spinoza and God, who "seems the infinite extended universe of being, law, and sequence, and has no purpose beyond itself." And so to the abiding religiosity of the writer.

> In childhood, in boyhood intermittently, through youth and all the following years, I kept the habitude of prayer. It is still with me as a way of communion, a turning to the great Companion.
>
> My life has been precious, wonderful, a thing to be grateful for to some Donor. I cannot think of myself as put together chemically or mechanically by "natural law." I must have a Cause that is all that I am.

Nothing here in this philosophical work to enlighten the epistomologist struggling to know what we know, nor yet to resolve the perplexities of the youth contemplating companionate marriage. Still, it is the authentic record of a mind that has achieved both knowledge and contentment.

* * *

THE STORY OF HAIR. *Its Purpose and Preservation.*

By Charles Nessler. *Boni and Liveright*
$2.50 $5\frac{1}{2}$ x 8; 277 *New York*

The author of this entertaining and instructive volume was formerly president of the American Master Hairdressers Association. Loquacious barbers are all too common; philosophical ones in the Johnsonian sense are occasionally to be found; but in hair-cutting, just as in every other line of human endeavor, a Newton or an Einstein only happens once in generations.

We shall let Mr. Nessler tell himself of his outlook and achievements.

> When I, a boy of seventeen, following several years of youthful interest in the vagaries of human hair, went to work in a coiffeur's shop, the hairdressing profession had the status of an art or a trade—the designation in any instance depending upon the individual's skill. Today, after the passage of two decades, the treatment of human hair is in the process of becoming a science, a field of study that is full of

> tremendous and hitherto unrealized possibilities, with social implications of far-reaching importance. To help it to this status, I have written this book, which represents many years of consistent research.
>
> Between the day when I began to learn at first hand about the phenomena of human hair, and the time in which I have been writing this book, many things have happened in my chosen field of research. Indeed, many of these things I have helped to happen. The physical and mental sciences have been my aids, and the new viewpoints on the subject of human hair which I set forth here have been the result of the combination of scientific and psychological study.
>
> In 1905, I brought forth my invention of the permanent wave, and when the late Professor Elie Metchnikoff witnessed a demonstration of it, he declared it to be the greatest advance ever made in hair science. Twenty years later came still another and vastly more important discovery, that of the classification of hair according to texture.
>
> To achieve these forward steps, I personally observed, treated, and experimented with hair from thousands of heads. Simultaneously I had an opportunity to study the mental characteristics of those whose hair came under my notice, and to observe the relationship between the fundamental nature of the individual and the covering of his scalp. For years, in many countries and among many classes of people, I have sought the truth about human hair. I have been on terms of intimacy in every stratum of society. I have visited innumerable institutions—hospitals, orphanages, prisons, schools and factories, studying the relationship between the individuals I have found and the hair of their heads.
>
> With the passage of years, observations became theories, and theories verified themselves until they became conclusions. My hair research left the field of science and entered the realm of psychology. In the last two decades there has been a tremendous advance in knowledge of psychological makeup of humankind. The behaviorists and the psychoanalysts have opened up new thought channels and new sources of understanding. To a world newly made aware of itself, I declare now that human hair is more than an adornment and appendage to mankind. It has serious meaning, and its importance to progress of the race cannot be underestimated.

What we like best in this modest recital of an obviously great accomplishment is the careful and precise distinction which Mr. Nessler repeatedly draws between psychology and science. What better guarantee could one have of his intelligence and insight?

The temptation to quote further from this book is great. We genuinely regret that lack of space forbids it, for we do like, when we can, to amuse as well as instruct the readers of The Quarterly Review of Biology.

In closing this notice, however, we want to say, quite seriously, that this book is well worth reading by anyone interested in the study of human constitution. It contains, along with much nonsense, a great deal of probably sound information about human hair which is unknown to most biologists and medical men.

INFANCY AND HUMAN GROWTH.

By Arnold Gesell. *The Macmillan Co.*
$3.50 5 ⅝ x 8 ½; 418 *New York*

The author's purpose is to give an account of the development of human behavior and mentality during infancy. He presents a normative schedule of infant behavior at given ages, based on clinical observation of infants under controlled conditions. It is his thesis that the behavior of infants tends to develop uniformly, so that infants of a given age will show similar characteristic behavior in all items observed. On this point we find that the mothers with whom we have discussed the behavior of infants are not in agreement with the author: their statements are to the effect that normal infants vary greatly in the relative development of different behavior items, so that, for example, child A will talk long before he walks, while child B will walk long before he talks. Of course, such observations have small scientific importance when they are in opposition to the conclusions reached in the psychological laboratory.

The author uses some very high-toned language; but he usually supplies a translation. For example, he says:

"The living eye can see but it cannot record. Not even in the visual arcana of the most eidetic cortex can permanent immutable images be stored for retrospective reference. This is just what the camera can do for us."

Again, he says:

"To some extent, then, the methodology of the observation of growth depends upon adjusting the durational interspaces between cross-sectional surveys of behavior levels in such a way as to yield a picture of the course of development."

This seems to say nothing more than that the intervals between observations should be of proper length; but it says it much more impressively.

THE CIRCLE AND THE CROSS. *A Study in Continuity. In two volumes. Vol. I.—The Circle.*

By A. Hadrian Allcroft.

Macmillan and Co.
12 s. 6 d. net *London*
5¾ x 8¾; viii + 370

In this book the author gives the results of his studies on the derivation of the word church. It is a long path from the church yard of the Christians of the British Isles of the tenth century back to the mound moot of the Cymbrians of prehistoric times, but the author has traversed it with much skill and infinite pains and here presents in great detail his results. Because of this mass of detail the book will be of interest especially to the student of archaeology.

The author starts with the premise that the ground upon which stands a sacred building must be older than such a building. Therefore it is in the names given to such areas that he traces the origin of the word *church* although it is only in the final chapter that he arrives at a discussion of this word. The bulk of the book is taken up in tracing the circular church yards of the tenth century back to the mound barrows (burial places of the early Christians and pagans) and the sepulchral rings. These in turn he relates to the stone circles of the Cymbric Celts, which were used by them as moots, and finally to the older form of moots—the mound moots, or "hills of ceremony."

Having reached this goal the author proceeds to show how it is possible that the word church has come from the words *cruc* or *circ*, names, that the early peoples gave to the structures which were used for ritualistic or administrative purposes.

There are several plates and many text illustrations showing the various types of circles and mounds found in the British Isles.

THE DEAF-MUTE POPULATION OF THE UNITED STATES. 1920. *A Statistical Analysis of the Data Obtained at the Fourteenth Decennial Census.*

Bureau of the Census.

Government Printing Office
25 cents *Washington*
5¾ x 9⅛; 159 (paper)

The census enumerator has as part of his duties in collecting data for the decennial census that of obtaining certain records on all deaf mutes in the country. This volume is a statistical analysis of such data (1920 Census). Deaf mutes, as recorded, range from "those partially deaf, but able to hear only with ear trumpets or other mechanical devices" to "those literally unable to hear or speak."

The correspondence method was used in collecting the data.

Male deaf mutes, as in all previous censuses, are shown to be in excess of female deaf mutes. An analysis in age groups, however, shows that in childhood and youth there are more female deaf mutes than male; during early and middle adult life the males exceed the females; and in old age there is a return to an excess of female deaf mutes. The records giving an analysis of congenital deafness in the different races are interesting. The negro furnishes a larger proportion (56.4 per cent) of deaf mutes than any other race. Other plans of this study include marital conditions, education, methods of communication, economic conditions and causes of deafness. One hundred statistical tables are scattered throughout the text.

It is of interest to note that, according to the report, in those years (1880, 1890, and 1900) when the enumerator received five cents additional pay for each deaf mute reported on a supplemental schedule, the returns in deaf mutes were probably more complete than in the following years (1910–1920) when no additional pay was allowed.

FIRST REPORT OF THE PREHISTORIC SURVEY EXPEDITION. *The Oriental Institute of the University of Chicago Communication No. 3.*

By K. *S. Sandford and W. J. Arkell.*

University of Chicago Press
$1.00 7 x 9½; 52 (paper) *Chicago*

This report is intended to relieve the hypothetical layman who may be curious as to the *raison d'être* of a prehistoric survey in Egypt. The particular expedition dealt with here is part of the Prehistoric Survey of the Nile Valley and Western Asia organized by the Oriental Institute of the University of Chicago, and was to place special emphasis on the study of the geological record in Egypt. Most of the report is given over to an account of the prehistoric discoveries that have been made in Europe, and to an explanation of the blessings that would accrue to science if these could be correlated with findings on the African continent. The rest deals with the laborious journey of the two explorers southward from Cairo as far as Assuan, their return to Luxor by way of the east bank of the Nile, and their observations *en route*. At Koseir, on the coast of the Red Sea, human artifacts were discovered in this region outside the Nile Valley for the first time. There are a number of rather poor photographs, showing off mainly the vehicles of the expedition, a seven-horse-power Jowett and a Ford tourer, the Ford most of the time in trouble.

THE UNITED STATES OF AMERICA. *Studies in Physical, Regional, Industrial, and Human Geography.*

By Albert P. Brigham.

Oxford University Press
$3.00 5½ x 8⅝; x + 308 *New York*

This volume is the outgrowth of a course of lectures given at the University of London in 1920. Its motive is to give a general view of leading facts and principles of American geography. In the mind of the lay reader the word "geography" will probably arouse all of his early dislike of what has been in the past a dull subject. The introductory chapters over, however, there is much about the United States that is of general interest, especially in the sections on distribution of population, racial composition, growth of manufactures, the statehood complex, etc.

In the chapter devoted to traditions and language the author lays great emphasis on our debt to Great Britain and his belief that the deep sea of Anglo-Saxon tradition will absorb all that is alien to the principles and ideals which have been inherited from England through our Puritan ancestors. Was he trying to make out a case for his country before a British audience, or perhaps making a bid for an extra-special dinner in his honor, when he said: "Nothing is so fundamental to America as the demand for liberty, justice and order, in private and public life. The will to enjoy these blessings came with the founders from over the sea, and it has survived all the changes of circumstance, the pressure of environment and the mingling of new elements of population. The common law of England lies beneath us today."

VILFREDO PARETO. *Sa Vie et Son Oeuvre.*

By G. H. Bousquet. *Payot*
20 francs 5½ x 8⅞; 230 *Paris*

Vilfredo Pareto was, we believe, one of the very great men of our time. His work is little known as yet, but we have no doubt that knowledge and appreciation of it will spread for a long time to come. Beginning as an economist under the influence of Walras, he brought the mathematical theory of economic equilibrium to something like a final form. From economics he moved into sociology, impelled, one imagines, by the impossibility of describing human behavior purely in economic terms. His sociological writings aim at interpreting the behavior of men as social beings largely in terms of the fundamental non-logical motives which drive them.

His work is the most impersonal and detached with which we are acquainted; we doubt that anyone can find, in the *Sociologie Générale*, evidence on which to determine Pareto's opinion as to any of the questions about which men fight. He is nearer to the purely scientific observer than any other writer we know of.

The present volume contains a brief account of Pareto's life, and a summary of his work. It has considerable value as an introduction to Pareto's work, because of that distinguished author's carelessness with regard to literary form. There is a bibliography of Pareto's writings.

DIE RASSE IN DEN GEISTESWISSENSCHAFTEN. *Studien zur Geschichte des Rassengedankens.*

By Ludwig Schemann. *J. F. Lehmanns*
18 Marks (paper) *München*
20 Marks (cloth)
6 x 8¾; xvi + 480

A dull and pedantic treatise, with 1195 footnotes. It constitutes the first of three volumes to be devoted to a general evaluation of race and races. The point of view is essentially that which was much more entertainingly expounded some years ago by a Frenchman named Gobineau. The author points out that since Gobineau no one has gone quite so surely and keenly to the root of the problem of races as have Madison Grant and Lothrop Stoddard. The book concludes on a high note: "*Wir sagten es zuvor: 'Die Germanen oder die Nacht' ist heute die Lösung wie einst. Der Beruf der Germanen kann nie und nimmermehr erlöschen, er wird—wenigstens in der Idee—fortbestehen bis ans Ende der Tage.*"

We break a usual editorial rule and let this stay in its original language. It sounds better. And what a comfort it is to know that ours is not the only land in which that pestilential microbe the One Hundred Percenter is endemic!

AGRICULTURAL SURVEY OF EUROPE: FRANCE. *United States Department of Agriculture, Technical Bulletin No. 37. By Louis G. Michael.*

Government Printing Office
25 cents *Washington*
5¾ x 9¼; 184 (paper)

The purpose and scope of these surveys are indicated as follows:

"The bulletins of the agricultural surveys of foreign countries will contain an analysis of the agricultural situation in each country from the viewpoint of the potential demand for agricultural products by those countries whose production is not sufficient to meet their national requirements and the nature and extent of the competition from foreign producers that the farmers of America must meet in disposing of their surplus in foreign markets. These surveys include a comparison between the prewar and postwar trends in the agriculture of the countries as affected by the economic conditions, territorial changes, if any, and other factors in each country, brought about by the World War."

THE LIFE OF A SOUTH AFRICAN TRIBE. *Vol. I. Social Life. Vol. II. Mental Life.*

By Henri A. Junod. *Macmillan and Co.*
50 shillings net *London*
5½ x 8½; Vol. I, 559
Vol. II, 660

These two volumes, a revised and enlarged edition of an earlier work, are by a member of the Swiss Romande Mission, who has lived many years among the northern clans of the Thongas of the Transvaal, and who has recorded for this particular tribe all that it was possible to learn concerning their manners and customs, their agricultural and industrial life, their art, religion and literature.

Although a missionary, the author has held himself strictly to the problem of placing on record all the information that he has been able to glean about the highly complex life of this group. Only at the very end of each volume under the heading of "Practical Conclusions" has he permitted himself to enter into a brief discussion of the various phases of their lives and the effect which the missionary and the white man has upon their *mores*.

Anthropologists will appreciate this new edition of a painstaking work, and the general reader who enjoys delving into books dealing with primitive peoples will find these two volumes highly interesting.

MY PEOPLE THE SIOUX.
By Luther Standing Bear.

Houghton Mifflin Co.
$4.00 5½ x 8; xiv + 288 *Boston*

This autobiography of a Sioux chief contains a certain amount of information relative to Indian manners and customs, but its main interest is as it illuminates the relation between the Indian and the white man. As set down by Standing Bear the asininity of the whites is appalling—especially in their efforts to be kind to the red men. His account of the early days of the Carlisle Indian School (he was one of the first pupils) is vastly entertaining.

It is to be hoped that some day the legend that Sitting Bull was responsible for the Little Bighorn massacre will be put down, but the hope is slim. Standing Bear does his best to give Crazy Horse the credit that belongs to him; he unaccountably omits mention of Gall.

OBSERVATIONS ON HAWAIIAN SOMATOLOGY.

Memoirs of the Bernice P. Bishop Museum Vol. IX, No. 4. Bayard Dominick Expedition Publication No. 13.
By Louis R. Sullivan (Prepared for publication by Clark Wissler).
Bernice P. Bishop Museum
$2.00 *Honolulu*
9½ x 12½; 76 + 5 plates (paper)

In this publication are given the compilations of data which were made by Dr. Louis R. Sullivan on living Hawaiians with the object of determining the "elements entering into this stock and in turn to suggest the position of Polynesians with respect to other races." Owing to Dr. Sullivan's death Dr. Clark Wissler prepared the material for publication, in order that it would be in such shape that future students of the Polynesians could make use of it. The tables, of which there are 57, consist of anthropometric measurements and data on qualitative characters. Since Dr. Sullivan left no usable notes Dr. Wissler has commented briefly on the results which the data show. The original individual records and a key to them are included in the publication. This work will be of great value to anthropologists who are especially interested in the Pacific Races.

AN ANTHROPOMETRIC STUDY OF HAWAIIANS OF PURE AND MIXED BLOOD.

Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University Vol. XI, No. 3.
By Leslie C. Dunn. Based upon data collected by Alfred M. Tozzer.
Peabody Museum
$1.75 *Cambridge, Mass.*
6¾ x 9½; 122 (paper)

There is in progress in Hawaii an extensive crossing of races, which offers obvious opportunities to the student of human genetics. In particular, extensive crossing is taking place between Hawaiian and Chinese, both of whom are probably relatively pure bred races, as human races go. The present anthropometric measurements are upon pure bred Hawaiians and upon crosses between native Hawaiians and other races. The numbers involved, when classified by sex, age, and race, form rather small series. The F_1 generation of Chinese ♂ × Hawaiian ♀, for example, contains only seven males and eleven females, which is, of course, wholly insufficient to warrant many conclusions.

The raw data from which the frequency distributions have been formed are given in an appendix.

JAWS AND TEETH OF ANCIENT HAWAIIANS.

Memoirs of the Bernice P. Bishop Museum Vol. IX, No. 3.
By H. G. Chappel.
Bernice P. Bishop Museum
$2.00 *Honolulu*
9½ x 12½; 20 + 4 plates (paper)

Crania in the Bernice T. Bishop Museum, in Honolulu, most of which were of the period preceding the coming of white men, furnish the material for this study of the teeth and dental diseases of ancient Hawaiians. Well formed teeth with excellent enamel were characteristic of these specimens. Traces of evolutionary change, variations in the two sexes, variability in the position of the mental foramen and irregularities in the cervical border of enamel are some of the topics treated statistically. A series of photographs exhibits the irregularities and diseases of the teeth. The work also included individual records of the mandibles and maxillae for both sexes.

AN EXPERIMENTAL STUDY OF THE EAST KENTUCKY MOUNTAINEERS.

A Study in Heredity and Environment. From the Psychological Laboratories of Harvard University and Duke University. Genetic Psychology Monographs Vol. III, No. 3.
By Nathaniel D. Mttron Hirsch.
Clark University Press
$2.00 *Worcester, Mass.*
6⅝ x 9¾; 56 (paper)

This interesting study of the East Kentucky Mountaineers has as its primary problem to discover the causes and conditions of the generally low mental status, as exhibited by intelligence tests, of the inhabitants of a region which was originally settled largely by people of Scotch-Irish descent. Other problems closely associated with the main theme, which the author considers, are pigmentation and cephalic index, migration, the degree of consanguineous marriages, size of family, etc. A number of tables give the results of intelligence tests and anthropological measurements.

FOLKLORE OF THE TEETH.

By Leo Kanner. *The Macmillan Co.*
$4.00 *New York*
5 ½ x 8 ½; xiii + 316

A collection of superstitions, charms, legends, and popular pathology and medicine relating to the teeth. We regret that in referring to legends of individuals furnished with double and triple rows of teeth, there is no mention of Paul Bunyan's logger, Double Jawed Murphy, who chawed up the grindstone in his sleep. His account of St. Appolonia, the patroness of toothache, is entertaining, but he displays a lamentable scepticism in doubting the authenticity of her relics, merely on the ground that more than thirty-two of her teeth are on display.

THE BUILDING OF CULTURES.

By Roland B. Dixon.
Charles Scribner's Sons
$4.00 6 x 9; x + 312 *New York*

This book deals with the origin and diffusion of human culture. It is well written, and gives a balanced discussion of the fundamental problems involved. Its outlook is primarily theoretical, but the practical applications of theory to concrete problems are not neglected.

The author is strongly opposed to the more extreme forms of the diffusion theory, and his criticism of such theories as those of Elliot Smith is severe; he seems to us, however, to make good his case. The book may be recommended to anyone interested in anthropology, whether a specialist or not.

HUMAN MERCHANDISE. *A Study of the International Traffic in Women.*

By H. Wilson Harris. *Ernest Benn, Ltd.*
6 shillings net *London*
4 ¾ x 7 ¼; 272

Mr. Harris has condensed and rewritten for popular consumption the two volume Report on the Traffic in Women and Children published by the League of Nations in 1927. The original report is a valuable source document for the student of human biology. This little "re-write" has only ephemeral value and not a great deal of that. England, the United States and Switzerland make the best showing relative both to domestic prostitution and to export and import traffic in women.

MORTALITY AND THE DRY LAW.

By Deets Pickett.
Research Department of the Board of Temperance, Prohibition and Public Morals of the Methodist Episcopal Church
$1.00 *Washington*
7 ¾ x 10 ⅜; 97 (paper)

A piece of brazen propaganda wearing a thin guise of objectivity. The data comprise mortality statistics under various categories from 1910 to 1926, organized for the ostensible purpose of revealing any relation between them and the operations of the prohibition law. All the results point to the healthy effect of the statute on mortality. The fallaciousness of some of the conclusions is obvious, of others more obscure. None would be accepted, on the evidence given, by a statistician endowed in the slightest degree with critical sense.

LA PÊCHE DANS LA PRÉHISTOIRE DANS L'ANTIQUITÉ ET CHEZ LES PEUPLES PRIMITIFS.

By A. Gruvel.
Société d'Éditions, Géographiques, Maritimes et Coloniales
40 francs *Paris*
6 ½ x 10; 232 (paper)

A discussion of fishing, as carried on in prehistoric times, in ancient history, and among modern primitive races. The author points out the importance of fish as a source of food among primitive races, and urges that the colonial administrators take measures to encourage its production and distribution. The book is abundantly illustrated.

ZOOLOGY

NATURE AND EXTENT OF FOULING OF SHIPS' BOTTOMS. *From Bulletin of the Bureau of Fisheries, Vol. XLIII, 1927, Part II. Document No. 1031.*

By J. Paul Visscher.
Government Printing Office
35 cents *Washington*
7 ½ x 11; 60 (paper)

A report of an investigation of the nature of fouling of ships' bottoms, and the conditions determining its extent. Some of the conclusions reached are:

> Fouling organisms are almost exclusively those commonly found on rocks and other submerged structures near shore, especially in harbors.
>
> Fouling occurs almost entirely while vessels are in port.
>
> Fresh water kills most of the organisms that cause fouling within 72 hours, but if calcareous or chitinous growths already have been formed, such materials remain and the resistance is not materially lessened.
>
> Certain species of barnacles grew at a very rapid rate, attaining a size of 2 inches and becoming sexually mature within 60 days.
>
> Certain barnacles are found attached on certain substances and in limited regions, indicating a relation between attachment and the nature of the surface.
>
> Light has been found to be an important factor governing the attachment of the larvae of the forms that cause fouling.
>
> At the time of attachment the larvae of *Balanus improvisus* and *B. amphitrite* are negative to light. (Most of the forms found on ships' bottoms probably are of a similar nature.)
>
> Light in the field of green and blue has been

demonstrated to have the maximum stimulating efficiency for the cyprid larvae of several barnacles.

This report indicates the value of an intensive study of seasonal periodicity of fouling organisms, of the relation between fouling organisms at the time of attachment and surface films, and a study of properly prepared paints of lighter colors than those now in general use.

KEY-CATALOGUE OF INSECTS OF IMPORTANCE IN PUBLIC HEALTH.

United States Public Health Service Hygienic Laboratory Bulletin No. 150.
By C. W. Stiles and Albert Hassall.
Government Printing Office
20 cents *Washington*
5 ¾ x 9; iv + 118 (paper)

A condensed, systematized compilation of the data of entomology as it applies to public health. It represents part 4 of Stiles and Hassal's Host Catalogue, Index Catalogue of Medical and Veterinary Zoology, prepared in special form for use at the Hygiene Laboratory. About a thousand entries alphabetically arranged are given and cross indexed with brief notes under the following headings:

A, biting insects; B, on cadavers or in graves; C, control of public-health pests; D, dermatology (lesions, dermatitis, eruptions, exanthema, parasites, urticaria); E, edible (food, drink); F, excreta; G, food and drink; H, jurisprudence; I, laity (fear, superstition); J, parasites and pseudoparasites (abdomen, ear, external, eye, head, intestine, miscellaneous, mouth, nose, stomach, subcutaneous, throat, and urinary system); K, pests (books, clothes, drugs, records, miscellaneous); L, pinching insects; M, poisons (arrows, defensive, food, spines, miscellaneous); N, pollution (air, water); O, stinging insects; P, therapeutics (lay, professional); Q, vectors (Aspergillus, bacteria, filth, Protozoa, Trematoda, Cestoda, Nematoda, Acanthocephala, Insecta).

THE SCORPIONS OF THE WESTERN PART OF THE UNITED STATES, *with Notes on those Occurring in Northern Mexico.*

By H. E. Ewing.
Government Printing Office
Washington, D. C.
6 x 9½; 24 (paper)

An increasing demand for information concerning the scorpions of the south-west region of the United States has led the Bureau of Entomology to undertake a study of these venomous arachnids. In this, the first bulletin issued on the subject, a taxonomic synopsis is given of all the species reported for the United States west of the Mississippi, an account of what is known of the distribution, life histories and habits of the more common species, and also of what is known of the effects of the venom. Notes are included concerning species occurring in northern Mexico.

Since no extended work on scorpions has been issued within the last twenty years, the plan of the author to make a comprehensive study of them will be welcomed not only by entomologists, but also by the inhabitants of the region and travellers in it.

LEAF-MINING INSECTS.

By James G. Needham, Stuart W. Frost and Beatrice H. Tothill.
The Williams & Wilkins Co.
$6.00 6 x 9; viii + 351 *Baltimore*

The authors "have endeavored to provide (1) an untechnical introduction to the study of leaf-mining insects, intelligible to the general reader; (2) an account of their natural history sufficiently detailed to be useful to the working ecologist; and (3) lists of the leaf-miners, of their food plants, and of technical papers concerning them adequate for the needs of the specialist. Thus we have undertaken to make more available to students, the rich but hitherto widely scattered results of many excellent investigations in this interesting ecological field."

The order is a large one; but the authors have succeeded remarkably well in their endeavor.

* * *

REPORT OF EUROPEAN CORN-BORER CONTROL CAMPAIGN BY THE UNITED STATES DEPARTMENT OF AGRICULTURE *for the Period March 14, 1927 to October 31, 1927, Inclusive.*

Government Printing Office
Washington
5 ¾ x 9; 24 (paper)

(Copies may be obtained free as long as the supply lasts from the Bureau of Entomology, United States Department of Agriculture)

This report gives an account of the large scale clean-up campaign against the European corn borer conducted during 1927. The cost of the campaign to the Federal government was $8,460,629.81; no figures are given of State or local expenditure. Annual surveys to determine the amount of infestation showed that at the close of 1926 there were approximately nine borers per hundred plants; at the close of 1927, after the clean-up there were approximately fourteen borers per hundred plants. "It therefore is obvious that the marked decrease in multiplication and the general improvement in corn-borer conditions recorded throughout the clean-up area at the close of the growing season of 1927 must be attributed principally, if not entirely, to the clean-up campaign."

It seems to us barely possible that this "decrease in multiplication" may have had other contributing causes.

* * *

THE FROG. *A Laboratory Guide.*

By Waldo Shumway. *The Macmillan Co.*
90 cents *New York*
4 ⅞ x 7 ⅜; viii + 67

The misfortune of the frog is that it is a "nice clean animal, easy to dissect and admirably fitted for physiological experiment." On some great dramatist—we would elect George Bernard Shaw—should be enjoined the duty of writing the epic tragedy of its immolation on the altar of science. This little manual furthers efficient and systematic dissection of the creature by the beginning student. The anatomical features to be noted as he progresses inward are given serially and directions for drawing are appended. There is a chapter on histology and one on embryology. It is not illustrated.

* * *

THE FISHES OF THE FAMILIES POMACENTRIDAE, LABRIDAE, AND CALLYODONTIDAE, COLLECTED BY THE UNITED STATES BUREAU OF FISHERIES STEAMER "ALBATROSS," CHIEFLY IN PHILIPPINE SEAS AND ADJACENT WATERS. *Contributions to the Biology of the Philippine Archipelago and Adjacent Regions. Smithsonian Institution, United States National Museum, Bulletin 100, Vol. 7.*

By Henry W. Fowler and Barton A. Bean.
Government Printing Office
$1.00 *Washington*
6 x 9 ¾; viii + 525 (paper)

This first part of a report on the immense collection of fishes made in 1907–1910 by members of the U. S. Bureau of Fisheries in the Albatross consists of studies on the fishes of the families Pomacentridae, Labridae, and Callyodontidae. Representatives of these families came chiefly from the waters of the Philippine Islands, although adjacent localities are included to some extent.

This work has been done with the utmost care. Extensive color descriptions made from the living material, or as soon after death as possible, add greatly to the value of the report. Forty-nine plates (uncolored) and a detailed index complete the volume.

THE SUGAR-CANE MOTH BORER IN THE UNITED STATES. *United States Department of Agriculture Technical Bulletin No. 41.*

By T. E. Holloway, W. E. Haley, U. C. Loftin and Carl Heinrich.

Government Printing Office
25 cents *Washington*
5¾ x 9¼; 77 + 2 plates (paper)

A description of the sugar cane moth borer (*Diatraea saccharalis*), with especial reference to its economic importance. It contains an account of the anatomy of the insect, as larva, pupa, and adult; the life cycle; natural means of control; and methods of artificial control. Indications are that the most effective method of control is the plowing under of the trash, rather than burning it, which is the procedure ordinarily used by the sugar planters. The authors' main objection to burning appears to be that it is more efficient as a means of destroying the egg parasites than the borers.

TRAITÉ DE ZOOLOGIE. *Fascicule VIII publié avec le concours de Rémy Perrier. Développement Embryogénique des Vertébrés Allantoidiens les Reptiles.*

By Edmond Perrier. *Masson et Cie*
40 francs *Paris*
6⅝ x 10; 2885–3115 (paper)

Since the death of Prof. Edmond Perrier in 1921 the editing of the remaining parts of his *Traité de Zoologie* has been taken over by his brother Rémy Perrier. The volume on batrachians appeared in 1925, and now we have the one on reptiles, which is preceded by a brief general account of the main features of the embryology of amniotic vertebrates. This is to be soon followed by volumes on the birds and mammals. When completed the whole will be a valuable addition to the basic text-book literature of zoology.

A STUDY OF PHYLLOXERA INFESTATION IN CALIFORNIA AS RELATED TO TYPES OF SOILS. *United States Department of Agriculture Technical Bulletin No. 20.*

By R. L. Nougaret and Macy H. Lapham.

Government Printing Office
10 cents *Washington*
5¾ x 9¼; 39 (paper)

The conclusion of this investigation into one aspect of the important question of the infestation of grape vines by *Phylloxera*, confirms previous general observation. Infestation rarely occurs upon soils of sandy texture and of loose porous structure, while it is most frequent where the soils are heavy, and become sticky when wet and bake and check when dry. The latter type probably affords more crevices and interstices for free movement of the insect. The study was executed on the vineyards of Fresno and Tulare Counties, California, which embody the most important types of soil in the State.

FUR-FARMING FOR PROFIT.

By Frank G. Ashbrook.

The Macmillan Co.
$4.00 *New York*
5 ¼ x 7 ¾; xxiii + 300

This book is written by one who has studied fur-farming from all angles. It contains much material of interest both to those engaged in this interesting field and to those contemplating entering it. The methods of raising the different animals, handling the pelts, marketing the furs, as well as reasons for success or failure are discussed. There is also a short chapter on legal considerations.

BIOLOGICAL AND TAXONOMIC INVESTIGATIONS ON THE MUTILLID WASPS. *Smithsonian Institution United States National Museum Bulletin 143.*

By Clarence E. Mickel.

Government Printing Office
65 cents *Washington*
6 ¼ x 9 ¾; ix + 351 (paper)

A detailed study of Mutillid wasps consisting of four parts: (1) Biology of the Mutillid wasps, (2) Type species of the genera of the family Mutillidae, (3) Monograph of the Mutillid wasps of the genus *Dasymutilla* occurring in America, north of Mexico, and (4) an annotated bibliography. Five plates and an index complete the volume.

WILD ANIMAL PETS.

By William L. Finley and Irene Finley.

Charles Scribner's Sons
$3.00 5 ¾ x 8; xiv + 311 *New York*

In this entertaining book is described the behavior of some twenty-four wild animals that were on a more or less social footing with the writers. The senior author, with many years of service as biologist and game warden of the State of Oregon, and his associate, have much to relate that will be of interest to people of all ages, but especially to the young who love the forests and the wild. There are numerous illustrations.

THE GIRAFFE IN HISTORY AND ART.

By Berthold Laufer.

Field Museum of Natural History
75 cents 5 ½ x 8 ½; 100 (paper) *Chicago*

In this little booklet the author gives many interesting facts concerning that oddly, not to say incredibly, constructed animal, the giraffe. The position which the giraffe has occupied in the art of the various peoples, from prehistoric times up to the present, is admirably shown by numerous illustrations. By no means the least interesting of these is a photograph of four superb creatures—prisoners in a kraal in their native country.

THE BOOK OF BIRDS. *Birds of Town and Country, the Warblers, and American Game Birds.*

Contains the following: *Foreword*, by Gilbert Grosvenor; *Common Birds of Town and Country, Friends of Our Forests—the Warblers, and American Game Birds*, by Henry W. Henshaw; *How Birds Can Take Their Own Portraits*, by George Shiras, 3rd; *Encouraging Birds Around the Home*, by Frederick H. Kennard; *Our Greatest Travelers—Migratory Birds*, by Wells W. Cooke; *The World Record for Feathered*

Friends, and Bird Banding, the Telltale of Migratory Flight, by E. W. Nelson.

National Geographic Society
$3.00 *Washington*
$6\frac{5}{8}$ x $9\frac{5}{8}$; 252

"In this revised volume are presented the principal articles and the most beautiful color illustrations of man's feathered friends which have been published in the National Geographic Magazine during the last thirteen years. The text and pictures comprise an authoritative and fascinating contribution to popular science."

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STUDIES IN TROPICAL WASPS—THEIR HOSTS AND ASSOCIATES (*with Descriptions of New Species*). *Entomological Series Bulletin No. 19.*
By Francis X. Williams.

Experiment Station of the Hawaiian Sugar Planters' Assoc.
$2.00 *Honolulu*
$6\frac{7}{8}$ x $10\frac{1}{4}$; 179 (paper)

Interesting notes, fragmentary, but not superficial, of the author's observations on wasps and their associates in limited regions of Queensland, Australia, the Philippine Islands, Ecuador, British Guiana and Brazil. There are a considerable number of diagrammatic illustrations, some photographs, and an index.

* * *

BOLLES LEE'S MICROTOMIST'S VADE MECUM. *A Handbook of the Methods of Microscopic Anatomy. Ninth Edition.*
Edited by J. Brontë Gatenby and E. V. Cowdry, with the collaboration of W. R. G. Atkins, Sir William Bayliss, J. Thornton Carter, Robert Chambers, W. Cramer, C. Da Fano, Helen Pixell-Goodrich, J. G. Greenfield, Reginald Ludford, and G. Payling Wright, F. W. Rogers Brambell.

P. Blakiston's Son and Co.
$7.50 *Philadelphia*
$5\frac{3}{8}$ x $8\frac{3}{4}$; x + 710

The ninth edition of this standard handbook of microscopic anatomy has been thoroughly revised and somewhat enlarged. There are new sections by Dr. Robert Chambers and Dr. W. R. G. Atkins. All students of histological technique will, as always, find this book an indispensable asset.

* * *

AN INTRODUCTION TO THE TECHNIQUE OF SECTION-CUTTING. *From the Notes of the Late Mr. Peter Jamieson. Edited by Frances M. Ballantyne.*

E. and S. Livingstone
3 shillings net *Edinburgh*
$4\frac{7}{8}$ x $7\frac{1}{4}$; 80

This book presents a connected account of the essentials of section cutting and staining, freed from the accumulation of detail to be found in the standard texts. For the beginner, it provides the foundation of a sound technique, and should be a valuable introduction to the subject.

* * *

QUANTITATIVE STUDY OF THE CHANGES PRODUCED BY ACCLIMATIZATION IN THE TOLERANCE OF HIGH TEMPERATURES BY FISHES AND AMPHIBIANS. *From Bulletin of the Bureau of Fisheries, Vol. XLIII, 1927, Part II. Document No. 1030.*
By Edward S. Hathaway.

Government Printing Office
10 cents *Washington*
$7\frac{1}{2}$ x 11; 24 (paper)

A careful study of the temperature tolerance of animals representing five different species. The results, which are given in detail, include a number of diagrams for each species studied exhibiting the effects of the varying temperatures on the different animals. A bibliography is appended.

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FISHES OF CHESAPEAKE BAY. *Bulletin of the United States Bureau of Fisheries Vol. XLIII, 1927. Part I.*
By Samuel F. Hildebrand and William C. Schroeder. *Government Printing Office*
$1.50 7½ x 10½; 366 *Washington*

A general account of the fishes of Chesapeake Bay with a systematic catalogue by classes and subclasses. There is a glossary of terms and a bibliography, but an index is lacking.

* * *

THE AMERICAN BATS OF THE GENERA MYOTIS AND PIZONYX. *Smithsonian Institution, United States National Museum, Bulletin 144.*
By Gerrit S. Miller, Jr. and Glover M. Allen.
Government Printing Office
55 cents *Washington, D. C.*
6 x 9½; viii + 218 (paper)

An exhaustive taxonomic account, indexed by generic, specific, and subspecific names.

* * *

A SERIES OF EIGHT RADIO TALKS ON ZOOLOGY, OLD AND NEW. *(With Select Bibliography.) Radio Publication No. 39.*
By Robert T. Hance.
University of Pittsburgh
5⅞ x 9⅞; 85 (paper)

Does one see a foreshadow of the university's doom in this booklet of radio talks? It represents the 39th radio publication issued by the University of Pittsburgh. Glancing through it we learn that under such headings as Animals that Never Were; Animals that Might Have Been; Natural History of Long Ago; A Muddled World of Living Things; Animals the Ancients Never Dreamed of; Through the Microscope; Wanderers of the Sea; and On the Trail of the Unknown, with a *Select Bibliography* as a final flourish, zoology was presented to the world at large from the University of Pittsburgh Studio of KDKA.

BOTANY

DER WASSERHAUSHALT ÄGYPTISCHER WÜSTEN- UND SALZPFLANZEN. *Vom Standpunkt einer Experimentellen und Vergleichenden Pflanzengeographie aus.*
By Otto Stocker. *Gustav Fischer*
12 marks 6½ x 9⅝; 200 (paper) *Jena*

This volume on the water regulation of desert and salt marsh plants is a good example of the trend of modern biology towards physico-chemical exactness in its observation and experimentation. Ecology can no longer be regarded as a pleasant pastime, to be cultivated as a means of taking the boredom out of long railway journeys and the like. The elaborateness of the physical and chemical measurements of environment and plants in this thorough study is impressive.

Many of the results are of great biological interest, but space is lacking to review them all here. For example the author finds that in these desert and salt plants of Egypt, with which he is dealing, the structural type of the plant itself is of greater importance than has been generally recognized in managing the water regulation. He shows that the fluctuation in surface transpiration of the single plant type from habitat to habitat is far less than that within the single habitat from plant type to plant type.

Altogether this book must be regarded as a contribution of first rate importance to the literature of ecology. There is an extensive bibliography but no index.

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ELEMENTARY BACTERIOLOGY.
By Joseph E. Greaves and Ethelyn O. Greaves.
W. B. Saunders Co.
$3.50 5¼ x 7¾; 506 *Philadelphia*

This book is designed for use as an elementary textbook. It will also be of use as a handbook of information to nurses, home demonstrators, agricultural and home economic workers, etc. The authors have succeeded in maintaining simplicity throughout, and have even excluded much of the ordinary garb of a textbook. There is very little that will be formidable to the lay reader. As comparatively little space is occupied with the illustrations, of which there are 129, the authors have succeeded in giving in the 500 pages a well rounded and entertaining picture of the science of bacteriology as it stands today. There is an index appended.

* * *

FACTORS OF SPREAD AND REPRESSION IN POTATO WART. *United States Department of Agriculture Technical Bulletin No. 56.*
By Freeman Weiss and Philip Brierley.
Government Printing Office
5 cents 5⅞ x 9; 14 (paper) *Washington*

The results of experimental investigations on the potato-wart fungus (*Synchytrium endobioticum*), accumulated by the authors while the disease itself was all the time becoming of diminished importance through effective control at the centers of infection. The experiments presented bear on the means of dissemination of the sporangia, their viability under natural and artificial conditions, and the susceptibility of the resting spores to heat and certain disinfectants.

* * *

THE BOOK OF WILD FLOWERS. *An Introduction to the Ways of Plant Life, Together with Biographies of 250 Representative Species and Chapters on our State Flowers and Familiar Grasses.* Contains the following: *Exploring the Mysteries of Plant Life,* by William J. Showalter; *Our State Flowers,* by Gilbert Grosvenor; *Familiar Grasses and their Flowers,* by E. J. Geske and W. J. Showalter; *Plant Biographies,* by William J. Showalter; *Color Plates from Life,* by Mary E. Eaton and E. J. Geske.
National Geographic Society
Washington D. C.
6⅝ x 9⅝; 243

"An introduction to the ways of plant life together with biographies of 250 representative species and chapters on Our State Flowers and Familiar Grasses." The volume is beautifully illustrated with color plates.

* * *

DIE NATÜRLICHE GRUPPE DER DAVALLIACEEN (SM.) KFS. *unter Berücksichtigung der Anatomie und Entwicklungsgeschichte ihres Sporophyten.*
By Enrique Pérez Arbeláez.
Gustav Fischer
6 Marks 6 ⅜ x 9 ½; 96 (paper) *Jena*

A thorough taxonomic revision of a group of the Polypodiaceae, with an abundance of morphological detail. There is a bibliography of 67 titles.

AMERICAN FORESTS AND FOREST PRODUCTS. *United States Department of Agriculture Statistical Bulletin No. 21. Prepared by the Forest Service.*

Government Printing Office
45 cents *Washington*
5 $\frac{7}{8}$ x 9 $\frac{1}{8}$; 323 (paper)

Statistics of forests, lumber production, pulp wood and paper production.

MORPHOLOGY

TRAITÉ D'EMBRYOLOGIE COMPARÉE DES INVERTÉBRÉS.

By C. Dawydoff. *Masson et Cie*
120 francs *Paris*
6 $\frac{1}{2}$ x 10; xiv + 930 (paper)

There has long been a need for a new and up-to-date textbook of reasonable size on invertebrate embryology. This need is now well met by this treatise of Dawydoff's. The presentation of the essential facts is simple and direct, and well adapted to student use. For each group there is a well chosen bibliography of original sources, by way of which teacher and student can go more deeply in the matter if they want to. The volume is, in effect, a French translation and adaptation by the author of a Russian text which he published in 1915. The book is illustrated with 509 text figures, and is well indexed. An English translation of it would make a welcome addition to our zoological teaching literature. But in the absence of such a translation every teaching zoological laboratory will want it on the shelves as a reference work.

OUTLINES OF SCIENTIFIC ANATOMY *for Students of Biology and Medicine. Designed to Supplement the usual Textbook Teaching.*

By Wilhelm Lubosch. Translated from the German by H. H. Woollard.

John Bale, Sons and Danielsson, Ltd.
21 shillings 6 x 9 $\frac{3}{4}$; 392 *London*

At the time the German edition was reviewed in a previous number of The Quarterly Review of Biology it was suggested that there should be an English translation made of this important work. This has now been done. Except for certain omissions and slight modifications, the translator follows very faithfully the original text. Its form is excellent.

For the benefit of those who are unacquainted with the German edition it should be said that this is not a textbook, but has as its purpose to supply collateral reading to students who are engaged in the necessary task of becoming acquainted with the large mass of facts which a study of anatomy entails. The science of anatomy is presented within its widest limits, from the morphological standpoint, and the interest and enthusiasm of the student cannot help but be aroused by the fascinating setting in which the subject is placed.

This book furnishes excellent material for a seminar course.

A HANDBOOK OF HISTOLOGY.

By A. McL. Watson.

William Wood and Co.
$3.75 4 $\frac{3}{4}$ x 7 $\frac{1}{4}$; xi + 207 *New York*

A triumph of epitome. The leaves of this book are small, the print large, the spacing and illustrations generous. Withal the subject of muscle is covered in 4 pages, blood in 6, nerve in 6, epithelium in 5, etc., with several somewhat longer chapters devoted to the other tissues. We fail to discern what good educational purpose is served by the superficiality, and didactic categorization that results from such condensation.

PHYSIOLOGY AND PATHOLOGY

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome III. Physiologie du Foie et de l'Appareil Urinaire.*

By M. Chiray, L. Cuénot, Ch. Dubois, I. Pavel, F. Rathery, G.-H. Roger.

Masson et Cie
70 francs 6½ x 9½; 751 *Paris*

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome IV. Les Sécrétions Internes.*

By J.-E. Abelous, R. Argaud, M. Garnier, J. J. Gournay, E. Hédon, L. Hédon, R. Huguenin, P.-M. Laignel-Lavastine, J. Parisot, G. Richard, G. Roussy, L. C. Soula, A. Tournade, R. A. Turpin.

Masson et Cie
65 francs 6½ x 9½; 585 *Paris*

This comprehensive treatise when completed will contain 11 volumes, divided as follows:

I. *Physiologie Générale*
II. *Digestion*
III. *Fonctions Hépatiques et Excrétion*
IV. *Les Sécrétions Internes*
V. *Respiration*
VI. *Circulation*
VII. *Les Humeurs: Sang et Lymphe, Réactions d'Immunité*
VIII. *Physiologie Musculaire. Chaleur Animale*
IX et X. *Physiologie Nerveuse*
XI. *Reproduction et Croissance*

Separate subjects are dealt with by individual authors, who are men of authority in their respective fields in the Latin countries.

Vol. III on the physiology of the liver and urinary apparatus comprises the following chapters: Physiology of the liver, by G.-H. Roger; Physiology of the gall bladder and of the bile ducts, by Chiray and I. Pavel; The "livers" of invertebrates, by L. Cuénot; Excretion, by L. Cuénot; Physiology of the kidneys, by R. Rathery; Excretion of the urine, and prostate, by Ch. Dubois.

Vol. IV on internal secretions contains the following chapters: General study of the internal secretions, by J.-E. Abelous; Pancreas, internal secretion, by E. Hédon and L. Hédon; The spleen, by J.-E. Abelous, R. Argaud and L.-C. Soula; The thymus, by J. Parisot and G. Richard; Thyroid gland, by Garnier and R. Huguenin; The parathyroids, by Garnier and R.-A. Turpin; The pineal gland, by Laignel-Lavastine; Hypophysis and infundibular region, by G. Roussy et J. J. Gournay; Superrenals by A. Tournade.

The printing and illustrations are rather poor. An index for the whole work is promised when it is complete, but there is none for the individual volume.

FILTERABLE VIRUSES.

By Harold L. Amoss, Jacques J. Bronfenbrenner, Alexis Carrel, Edmund V. Cowdry, Rudolf W. Glaser, Ernest W. Goodpasture, Louis O. Kunkel, Stuart Mudd, Peter K. Olitsky, Thomas M. Rivers. Edited by Thomas M. Rivers.

The Williams & Wilkins Co.
$7.50 5⅞ x 9; ix + 428 *Baltimore*

An attempt is here made to review our present knowledge of the biologic phenomena that are usually discussed under the head of filterable viruses. As the editor points out in his introductory article, our ignorance concerning the nature of these organisms is great, and no authoritative systematic account is yet possible. What is done here is to collect the opinions of a number of investigators on aspects of the subject with which they have had special experience. They are the following: Thomas M. Rivers—Some General Aspects of Filterable Viruses; Stuart Mudd—Filters and Filtration; Alexis Carrel—Tissue Culture in the Study of Viruses; Edmund V. Cowdry—Intracellular Pathology in Virus Diseases; Harold L. Amoss—Virus Diseases of Man as Exemplified by Poliomyelitis; Peter K. Olitsky—Virus Diseases of Mammals as Exemplified by Foot-and-Mouth Disease and Vesicular Stomatitis; Ernest W. Goodpasture—Virus Diseases of Fowls as Exemplified by Contagious Epithelioma (Fowl-Pox) of Chickens and Pigeons; Rudolf W. Glaser—Virus Diseases of Insects; Louis O. Kunkel—Virus Disease of Plants; Jacques J. Bronfenbrenner—Virus Diseases of Bacteria—Bacteriophagy.

If the work as a whole seems to be characterized by a measure of vagueness and inconsistency, it is to be said that this is true too of the subject itself. There is an extensive bibliography appended to each article and an index for the entire volume. It should be of service to biologists who are curious to learn of what is being done in the realm of the tiniest of living beings.

TRAITEMENT BIOLOGIQUE (BIOTHÉRAPIE) DES INFECTIONS *par les Huiles Essentielles, les Résines (Oléorésinothérapie), et par les Essences Déterpénées, les Lipides (Oléolipothérapie).*

By Albert Jentzer. *Masson et Cie*
80 francs 6¾ x 9¾; 424 (paper) *Paris*

This is a detailed account of an extremely thorough investigation of certain new therapeutic agents, which, on the evidence presented, appear to be of great value in all pyogenic infections (staphylococcus, streptococcus, B. coli, etc.). The author is *Privat-docent* in surgery at the University of Geneva. "Themsaline," the first and more important of the agents tested, is a rectified and fractioned mixture of certain essential oils, which has in its final composition 7 per cent phenols, 12 per cent aldehydes, and 63 per cent terpenes. A full account is given of its preparation. It is administered intravenously. Its results in cases of pyogenic infections, abscesses, phlegmons and the like, are little short of marvellous. The author gives extensive clinical and experimental reports on themsaline. Another agent, which under certain indications may be used with themsaline, is "lipodeterpenol," which functions as an antigen. Space is lacking for more detailed review of this book here, but we commend it to the attention of pharmacologists, surgeons and medical men, with the statement that it bears all the earmarks of a thorough and sound piece of research. There is a bibliography of 499 titles.

ÜBER DAS PROBLEM DER BÖSARTIGEN GESCHWÜLSTE. *Eine Experimentelle und Theoretische Untersuchung.*

By Lothar Heidenhain. *Julius Springer*
28 marks (paper) *Berlin*
32 marks (cloth)
10 x 13; vi + 153

This beautifully printed and illustrated quarto monograph describes the author's researches on the cause of cancer. It proceeds from the working hypothesis that it should be possible so to destroy human tumors by lysis that the agent in them which causes cancer would not be destroyed. Then the lytic products of such technique are to be injected into animals, and there should then be found in the body of such animals changes in the epithelial or connective tissue cells of carcinomatous or sarcomatous character. Heidenhain has tested this idea on 2521 mice, working with human tumors of various sites and histological types. The result is taken to confirm the hypothesis. In fact it was found that in white mice injected with derivates of human carcinoma (either primary or metastatic) or sarcoma, there appeared carcinomata or sarcomata. The author concludes that the relation between these events was causal, and concludes that cancer is an infectious disease.

This is a piece of work with which all students of the cancer problem will have to reckon.

COMPARATIVE PHYSIOLOGY OF THE HEART.

By A. J. Clark. *The Macmillan Co.*
$3.25 $5\frac{1}{4}$ x $8\frac{3}{8}$; v + 157 *New York*

The author of this volume devotes himself very largely to the comparative physiology of the vertebrate heart. After the introductory chapters the following aspects of the subject are treated: The properties of vertebrate heart muscle; the transmission of the excitatory process; the nervous control of the heart; influence of temperature on heart functions; the influence of body weight on the size of the heart in warm-blooded animals; the relation between circulation volume and body weight in warm-blooded animals; heart functions in cold-blooded animals and embryos; the work of the heart in relation to body weight in warm-blooded animals; and the influence of chemical environment on the heart's activity.

This book will be of interest to all research workers in biology, following as it does, the paths of many divergent lines of work. Each chapter is terminated with a bibliography. Included in the text are 49 tables and 15 figures. At the end of the book are three appendices containing various records on mammalian and bird hearts.

HISTORY OF THE PHYSIOLOGICAL SOCIETY DURING ITS FIRST FIFTY YEARS 1876–1926.

By Sir Edward Sharpey-Schafer.
Cambridge University Press
15 shillings net *London*
$6\frac{1}{2}$ x $9\frac{1}{4}$; 198 (paper)

At the meeting of March 21, 1925, of the Physiological Society of England, it was resolved that "Sir E. Sharpey-Schafer be asked to write a report on the foundation of the Society." The present volume is the result. It is a useful contribution to the contemporary history of science. The Physiological Society started as a dining club, and in some sense has always remained that. It has never had a president, and there is no provision in its statutes for any elaborate formal organization. The underlying motive which led to its formation was, aside from sociability, to provide some means for presenting a unified front on the part of experimental physiology against an impending legislative attack upon the practice of vivisection. The volume consists essentially of an abstract of the minute books of the Society, with brief running comments, largely biographical, by the author. It is thoroughly indexed.

COYOTILLO (KARWINSKIA HUMBOLDTIANA) AS A POISONOUS PLANT. *United States Department of Agriculture Technical Bulletin No. 29.*

By C. Dwight Marsh, A. B. Clawson and

G. C. Roe. *Government Printing Office*
10 cents *Washington*
5¾ x 9⅛; 26 (paper)

The subject of this bulletin is a shrub found in Texas and Mexico, and known since 1789 to possess poisonous properties. The effect of ingestion on cattle, sheep, goats, guinea pigs, and chickens, as shown by the prolonged experiments of the authors, is to produce a motor paralysis affecting chiefly the posterior limbs. The leaves as well as the fruit are toxic, but to different degrees. Symptomotology, toxicology and moto-pathology are considered, but nothing very enlightening as regards the character or location of the primary lesion.

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ETUDES SUR L'IMMUNITÉ DANS LES MALADIES INFECTIEUSES.

By A. Besredka. *Masson et Cie*
30 francs *Paris*
5⅝ x 8¾; 404 (paper)

In this volume are collected some fifteen of the distinguished author's studies on various aspects of the problem of immunity, made during the past thirty years at the Pasteur Institute in Paris. Dr. Besredka somewhat apologizes for their apparent diversity, but points out that there is really a unifying element in that they all bear upon the problem of vaccination, preventive or curative. All students of immunity will be glad to have this material handily collected in a single volume.

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L'INFECTION BACILLAIRE ET LA TUBERCULOSE CHEZ L'HOMME ET CHEZ LES ANIMAUX. *Processus d'Infection et de Défense. Étude Biologique et Expérimentale. Vaccination Préventive.*

By A. Calmette. With the collaboration of A. Boquet and L. Nègre. *Masson et Cie*
125 francs *Paris*
6½ x 10; 883 (paper)

The third edition in French of the definitive work by Calmette. The first edition in English translation was noted in these columns in an earlier number (Vol. I, No. 1). This issue is enlarged by the author with the assistance of A. Boquet and L. Nègre of the Institut Pasteur de Paris. The additions include an account of the work of foreign investigators and two notable chapters on active immunization with BCG.

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PRACTICAL BACTERIOLOGY, BLOOD WORK AND ANIMAL PARASITOLOGY *including Bacteriological Keys, Zoological Tables and Explanatory Clinical Notes. A Compendium for Internists.*

By E. R. Stitt. *P. Blakiston's Son and Co.*
$6.00 *Philadelphia*
5¼ x 7¾; xv + 837

The eighth edition of this very useful standard laboratory manual has been thoroughly revised and enlarged and brought entirely up to date.

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BIOCHEMISTRY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 258.* Containing the following articles: *Die äquimensurale Ultraviolett- und Fluorescenz-photographie*, by Gustav Kögel; *Die Methodik zur Prüfung der Lichtempfindlichkeit der Naturfarbstoffe*, by Gustav Kögel; *Methodik der diagnostischen und therapeutischen Anwendung der Elektrizität*, by August Laqueur.

Urban und Schwarzenberg
10 marks 7 x 10; 172 (paper) *Berlin*

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 261. Elektronen- und Ionenröhren.*

By Ferdinand Scheminzky.
Urban und Schwarzenberg
25 marks 7 x 10; 442 (paper) *Berlin*

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 262. Methoden der Bioelektrostatik.*

By Rudolf Keller and Joseph Gicklhorn.
Urban und Schwarzenberg
5 marks 7 x 10; 92 (paper) *Berlin*

These new parts of the Abderhalden *Handbook* of biological technique deal with various aspects of biophysics. They are all valuable contributions, but are calculated to throw the old-fashioned naturalist into a fit of depression at the realization, which they emphatically drive home, that at least a part of biology has got away from him, hopelessly and irrevocably.

CREATINE AND CREATININE.

By Andrew Hunter.
Longmans, Green and Co., Ltd.
\$5.00 6⅛ x 9⅝; vii + 281 *New York*

Creatinin stands in a unique position among excreted products in its probable relation to endogenous metabolism. While its great interest together with the chemically closely related creatin has long been recognized, their biochemistry remains obscure in most essential details. This volume adequately reviews our present knowledge of their chemistry and physiology and provides an extended bibliography. The recent fundamental experiments of Fiske and Subbarow indicatingthat creatin exists in the muscles as a labile compound with phosphorus awaken renewed interest in the subject and make this work especially timely.

A TEXT-BOOK OF BIOLOGIC ASSAYS.

By Paul S. Pittenger.
P. Blakiston's Son and Co.
\$3.00 net *Philadelphia*
5¼ x 7¾; xxiii + 373

In this reissue, the subject matter of the first edition (former title *Biochemic Drug Assay Methods*) has been practically rewritten, in order to include the numerous advances made in methodology; and several new chapters and 64 new illustrations added in order to bring the manual up to date. Its purpose is to serve as a text book of biologic assay technique for students of pharmacy and medicine, and for those engaged in laboratories devoted to the biologic standardization of drugs.

OILS, FATS AND FATTY FOODS. *Their Practical Examination. A Handbook for the Use of Analytical and Technical Chemists and Manufacturers.*

By E. Richards Bolton (with a chapter on Vitamins by J. C. Drummond).
P. Blakiston's Son and Co.
\$8.00 *Philadelphia*
6⅛ x 9¾; xvi + 416

This is a handbook for the use of technical chemists who are called upon to analyze edible oils and fats. The methods given are those which the author has found satisfactory. He has, in general, given only one method for any one purpose. After chapters on preliminary examination, on general analytical methods, and on the interpretation of analytical methods, there follow chapters on specific products, such as butter and margarine, animal fats, vegetable oils and fats, cocoa and chocolate, and milk. There is a final chapter, by Drummond, on the nutritive value of fats and oils, with particular reference to vitamins.

LABORATORY MANUAL OF PHYSIOLOGICAL CHEMISTRY.

By Meyer Bodansky and Marion S. Fay.
John Wiley and Sons, Inc.
$2.00 5¾ x 9; 234 *New York*

Pedagogical experiments for the student in the classical course of physiological chemistry. The importance of dynamical concepts that is emerging from the modern investigations into the physical chemistry of the organism is not reflected in the examples. Neither sodium nor potassium is listed in the index.

STUDIES ON OXIDATION-REDUCTION. I–X. *Hygienic Laboratory Bulletin No. 151.*

By the Staff of the Division of Chemistry, Hygienic Laboratory, United States Public Health Service.
Government Printing Office
50 cents *Washington*
5⅞ x 9⅛; vi + 363 (paper)

The first ten papers on oxidation and reduction of Clark and his associates at the Hygienic Laboratory are here reprinted. The first two develop the essential equations for the electrode potentials, and the rest deal with specific organic oxidation-reduction systems. The whole work is of fundamental import for the understanding of the mechanics of living processes.

SEX

TECHNIQUE OF CONTRACEPTION. *The Principles and Practice of Anti-Conceptional Methods.*

By James F. Cooper. *Day-Nichols*
$7.50 *New York*
6⅛ x 9⅛; xvi + 271

The preface makes the following statement:

> The contents of this book and its technical presentation indicate clearly that it is written exclusively for the medical profession. Moreover, the author has specifically arranged with the publisher so that copies of the book will be available only to physicians, thus giving emphasis to his belief that all practical aspects of contraception should be under the direction of members of the medical profession.

The book contains one of the first attempts at a statistical investigation of the efficiency of contraceptive methods which has ever been published. (Dr. Marie Stopes' report on the first five hundred cases at her clinic is valueless because of the failure to follow up cases.) He reports 95 per cent successful cases out of a total of 806 patients who had been using the methods prescribed for a period of six months to two years. There is, however, no evidence to show how many babies these women would have had during the observed period of exposure to risk if they had *not* used the specified methods of contraception. The chief cause of failure was said to be carelessness; and we are inclined to wonder whether any higher percentage of success than that alleged could reasonably be expected in ordinary clinical experience. But what Cooper, and nearly all birth control propagandists, mean when they speak of "success" is merely that the women under observation did not become pregnant during the time they were observed. This fact, however, obviously is no proof that failure of conception was *caused* by the contraceptive technique employed.

GREFFE OVARIENNE ET ACTION ENDOCRINE DE L'OVAIRE. *Étude Histologique, Biologique, Clinique et Chirurgicale.*

By Vittorio Pettinari. *Gaston Doin et Cie*
70 francs 6$\frac{1}{4}$ x 9$\frac{1}{2}$; 487 (paper) *Paris*

Works on ovarian and testicular grafts suffer in these times from the suspicion of the ordinary reader that probably here is another piece of quackery. One is disposed to be a little more severely critical than of a work in some other fields of research. With the ultimate validity of the author's conclusions we do not propose to deal here. Some of them sound plausible enough; others are rather more disturbing to our *a priori* sense of the fitness of things. We do wish, however, to regret that the author has not seen fit to describe in more detail the experimental evidence on which his conclusions rest, and particularly that he has stated so little as to the number of experiments involved. We find him stating that he has operated on 332 animals (over 350, he says, at the time of going to press); and this may be a large number, but its significance depends on the ground covered. Now he also makes some statements as to the nature of his experiments, and to the variables considered; and at rough computation, to cover completely the ground indicated, a total of something on the order of a thousand experiments would have been required, allowing only one for each combination of variables. Accordingly, in the absence of any statement of the extent of the experience on which any particular conclusion rests, one is somewhat at a loss for an indication as to the validity of any of the work.

Our general attitude of hesitancy is not lessened by the author's work on rejuvenation. His general conclusions agree with those of Voronoff; but as far as one can learn, the experimental basis on which they rest is very thin indeed.

The book is largely and well illustrated with drawings and photographs of ovarian sections. There is a bibliography, restricted, however, to the literature on actual ovarian grafts.

* * *

SEX DEVELOPMENT IN APES. *Comparative Psychology Monographs Vol. 5, No. 1.*

By Harold C. Bingham.

The Johns Hopkins Press
$2.50 7 x 10$\frac{1}{4}$; 165 *Baltimore*

It has been noted by that eminent anthropologist, George Jean Nathan, as one of the folk beliefs of America, that when one takes one's best girl to the Zoo, the monkeys invariably do something that is very embarrassing. The present monograph is intended to substantiate that belief. It gives an extended account of the beginnings of sex behavior in the two pairs of young chimpanzees of the Yale Institute of Psychology, together with some observations on adults at the Abreu colony. The monograph is of great interest to psychologists, and, we regret to say, to laymen.

* * *

SEXUALTYP UND KULTUR. *Elemente einer Darstellung der europäischen Kulturgeschichte auf der Grundlage der vergleichenden Psychologie der Geschlechter. Abhandlungen aus dem Gebiete der Sexualforschung. Band V, Heft 3.*

By Ernst Klimowsky.

A. Marcus und E. Weber's Verlag
6 marks 6$\frac{7}{8}$ x 10; 80 (paper) *Berlin*

The author's position is that nearly all human beings are not wholly single-sexed, male or female, in the makeup of their personality, and particularly with reference to the psychological panel of personality, to use Draper's convenient terminology. Klimowsky discusses in an interesting, if somewhat pedantic manner, the influence upon cultural history of these phenomena of human intersexuality, composite sexuality, etc. The work is heavily documented, there being some 125 notes to the literature.

PSYCHOLOGY AND BEHAVIOR

THE UNCONSCIOUS. *A Symposium.*

Alfred A. Knopf, Inc.
$2.50 5 x 7⅜; 260 *New York*

This book is the result of a symposium, held in Chicago under the auspices of the Illinois Society for Mental Hygiene, which had for its aim the study of the synthetic tendency in the unconscious. We read in the preface by Mrs. W. F. Dummer that it is by a "chewing of the mental cud" that scientific principles are formulated and poets inspired, as well as many of the very ordinary affairs of life regulated. Therefore "May we learn consciously to utilize this integrative action of the unconscious? May we find the basis of constructive ideation with resultant progressive behavior? Is thought process discoverable?"

The opening chapter is on "The Beginnings of Unity and Order in Living Things" by the well-known biologist, C. M. Child; followed by a paper "On the Structure of the Unconscious" by Kurt Koffka; The Genesis of Social Reactions in the Young Child, by John E. Anderson; The Unconscious of the Behaviorist, by John B. Watson; The Unconscious Patterning of Behavior in Society, by Edward Sapir; The Configurations of Personality, by W. I. Thomas; The Prenatal and Early Postnatal Phenomena of Consciousness, by Marion E. Kenworthy; Values in Social Psychology, by F. L. Wells; and Higher Levels of Mental Integration, by William A. White.

The various chapters make interesting reading although the reader is left with the impression that much violent "chewing of the mental cud" is still necessary if the unconscious is ever to be brought out into the open and consciously used as a means to an end. And even then, shall we not have just as many mentally inefficient people in the world, or, possibly even more? Would not Dr. Watson's plan produce a far greater crop of neurasthenics than we are already burdened with?

MORTON PRINCE AND ABNORMAL PSYCHOLOGY.

By W. S. Taylor. *D. Appleton and Co.*
$1.75 5 x 7⅜; xi + 137 *New York*

This is a brief connected account and summary of the theories of the leading American psychopathologist. It should be read by anyone who has read Freud and swallowed him whole.

MALARIAL PSYCHOSES AND NEUROSES *with Chapters Medico-Legal, and on History, Race Degeneration, Alcohol, and Surgery in Relation to Malaria.*

By William K. Anderson.
Oxford University Press
$13.00 7¼ x 9¼; viii + 395 *New York*

This treatise surveys the aspects of malaria that relate to its nervous manifestation. Dealing largely with matters of detail, the author succeeds nevertheless in retaining throughout a sense of the broad social interest of his subject. The more general deteriorating effects of the disease on society are first discussed, and then its minute neuro-pathology. Then the psychic manifestations are considered *seriatim*, under the several classical psychopathological categories, by means of brief case histories. Neuropathology is similarly considered. The illustrations are not numerous, but the colored plates depicting the cellular pathology are superbly reproduced, and the style measures up to the high standard we have learned to expect in the Oxford publications. There are some thirty-five pages of references, and an index of authors and subjects.

GORILLA. *Tracking and Capturing the Ape-Man of Africa.*

By Ben Burbridge. *The Century Co.*
$3.50 5⅛ x 7⅞; xi + 323 *New York*

The portion of this book which will be of the greatest interest is that dealing with the author's expedition into the Belgian Congo, from which he brought back the only live gorillas in captivity. In particular, the young female, "Congo," who has been studied in considerable detail by Professor Yerkes, was captured by Mr. Burbridge. His account of the wild life of the gorilla is interesting, if not extensive. Aside from the gorillas, the book does not differ greatly from the ordinary account of African hunting trips.

BIRDS AT THE NEST.

By Douglas Dewar.
John Lane: the Bodley Head Ltd.
7 s. 6 d. 5 x 7⅜; 271 *London*

Douglas Dewar's books about birds always contain a good deal of material of general biological interest. The present volume is no exception to this rule. It discusses a considerable amount of material derived from the literature and from personal observations in the field regarding bird behavior, particularly with reference to the reproductive cycle. The net result of the discussion is to explode a great many rather widely held notions as to the intelligence of wild birds. The book is pleasantly written, and well indexed.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE NEW GENETICS.

By Glenn C. LaMaster. *Glenn C. LaMaster*
$1.50 *R.F.D. 2, Box 48, Akron, O.*
6 x 9; 80 (paper)

Those Ishmaelites in the society of science who bear the noble title of "cranks" are to be numbered among our few really independent intellects. Neither authority, nor accumulated wisdom, nor the rules of logic, stem the free movement of their thought. The emotional thrills that reward their anarchic rebelliousness must remain lost to the laboratory slave who has been taught to yield his most fundamental opinion to the position of a decimal point. But if he can overcome an habitual squeamishness, and plunge himself heartily into some of their literary products, he is certain to be rewarded by entertainment, and may occasionally pick up a fruitful idea.

The interest of this author in genetics springs from his occupation with poultry breeding on a farm near Akron, Ohio. His doctrines, if we may judge from references, are the product of some good reading and a lively imagination. We open to an introductory thesis, the guiding idea of the principles later enunciated. "The spermatozoon is the seedling of a new brain and nervous system, and that the heart and venous system is given to the offspring by the mother parent." The writer considerately refrains from burdening the reader with too much evidence, but Fig. 2 goes far toward complete proof. It shows in sagittal section the human brain with its appended nerve cord tapering off as it winds caudally to a thin point; and in juxtaposition a pen sketch of a spermatozoon, the massive head merging into the long thin undulating body. "Its (the spermatozoon's) activity proves without question that it is endowed with consciousness." "Compare the shape and form of the brain and spinal cord with the shape and form of the spermatozoon." After a while in ontogeny "The spermatozoa bud off from the ends of the nerve branches in the glands after the same plan that seeds are produced upon the ends of the branches of trees." On the other hand, "The ova of the female bud off from a branch of the venous system in the ovaries." "Life begins with the union of the spermatozoon with the heart in rudimentary form. This union takes place in a microscopic sea where abound great numbers of basic body tissue cells which always exist in loose affinity in the germ plasm of both sexes." So we have acquired the nervous and vascular systems.

> Now in respect to the several different kinds of cells that enter into the body organism other than the nervous and venous systems, how are they formed for the reproduction process? It seems very certain that these cells all exist in the germ plasm of both sexes. These cells which make up the main body structure are each one an independent life by itself. In the body structure they mass together in great bundles as we see in the muscles. But in the germ plasm of the glands these cells exist and multiply in loose affinity.

We go on to deeper matters, sex. "This difference of sex is determined by which unit, the venous system or the nervous system, first gains possession of the glands. Thus there is a struggle between these two units to determine which will dominate the sex of the embryo." After a clear explanation of Mendelism and segregation, we get the explanation of dominance.

> Cells are of different kinds and from different individuals possess different degrees of vitality. And because of their different degrees of vitality and different traits of character, they have different rates of reproduction. And because of these differences some cells will divide twice as fast as others, and in some instances even greater differences in rate of reproduction may exist. . . . Suppose that two cells of different character start reproducing in the first stage of the embryo, and suppose that one cell possessing the factor which I will call the A factor reproduces twice as fast as the other cell which contains the B factor. . . . When we consider the fact that cell reproduction takes place at a very rapid rate and that there are many trillions of cells in an adult human body, it is plain that long before the body was mature the B factor would be completely obliterated from visible detection, and the A factor would appear as a dominant factor.

There is more of this, leading into practical advice to breeders of fowl and men, which we are unable to give for lack of space. Trained biologists will find some of these ideas novel, but this point is covered in the text. "The new facts of reproduction and inheritance are given to breeders here for the first time."

THE EVOLUTION OF SCIENTIFIC THOUGHT FROM NEWTON TO EINSTEIN.

By A. d'Abro. *Boni and Liveright*
$5.00 5½ x 8⅝; xx + 544 *New York*

So far as may be judged by an amateur mathematician, this is the most satisfactory book issued for the layman to date on relativity and associated subjects. One must not conclude at once that it is altogether easy reading. To begin with it contains over 500 closely printed pages, and the context is not always obvious at first glance.

> In the case of a fluid of the density of water, calculation shows that when the sphere of water had attained a radius of about 400 million kilometers, it would be impossible to increase its size further by adding more water to it. When this critical volume was reached, the fluid would fill the spherical space entirely. Moreover, calculation shows that the flow of time would be arrested altogether at the surface of the fluid, so here again we have another reason which would prevent the sphere from growing any larger.

But it is thorough; the author appears to have a real grasp of his mathematics, and he has an instinct for what will be the logical difficulties of the careful general reader. We are personally grateful for relief on one point that has oppressed us ever since we read an account by Einstein himself. It will be recalled that according to the Special Theory, in a system B moving with constant velocity relative to A, time is slowed up, so that an individual on B will appear younger than his twin brother on A. But these relationships are reversible and the individual on A will appear the younger from the viewpoint of B. It occurred to us therefore that if B took a trip around a circle and returned to A, when the brothers met they would be younger than each other. The dilemma is considered at length by the author, and the difficulty is resolved when it is realized that to travel in a circle B would have to accelerate, and acceleration takes us into the General Theory. Here it is not legitimate to make arbitrary transfers of the axes of reference. An accelerating system stands in a unique position and one may not transfer to such a system without positing a gravitational field. When this is done all calculaitons are consistent. B is younger from either viewpoint.

This should interest biologists. It appears to say that if an organism gets itself surrounded by a gravitational field, its life processes will all be slowed up. And since (so it appears to us) this must be due to physical forces, it becomes conceivable that one may influence the rate of life by physical means. The speculation serves as a corrective of another error, readily made by the reader of superficial accounts of relativity, namely that it is essentially only a matter of viewpoint that is involved. The fact is that if relativity be true, not only are our conceptions profoundly affected, but the physical world is fundamentally and actually different.

The inherent difficulty of the reading is aggravated by the poor and small print of the book, and the lack of an index is a serious defect.

* * *

THE RÔLE OF SCIENTIFIC SOCIETIES IN THE SEVENTEENTH CENTURY.

By Martha Ornstein.

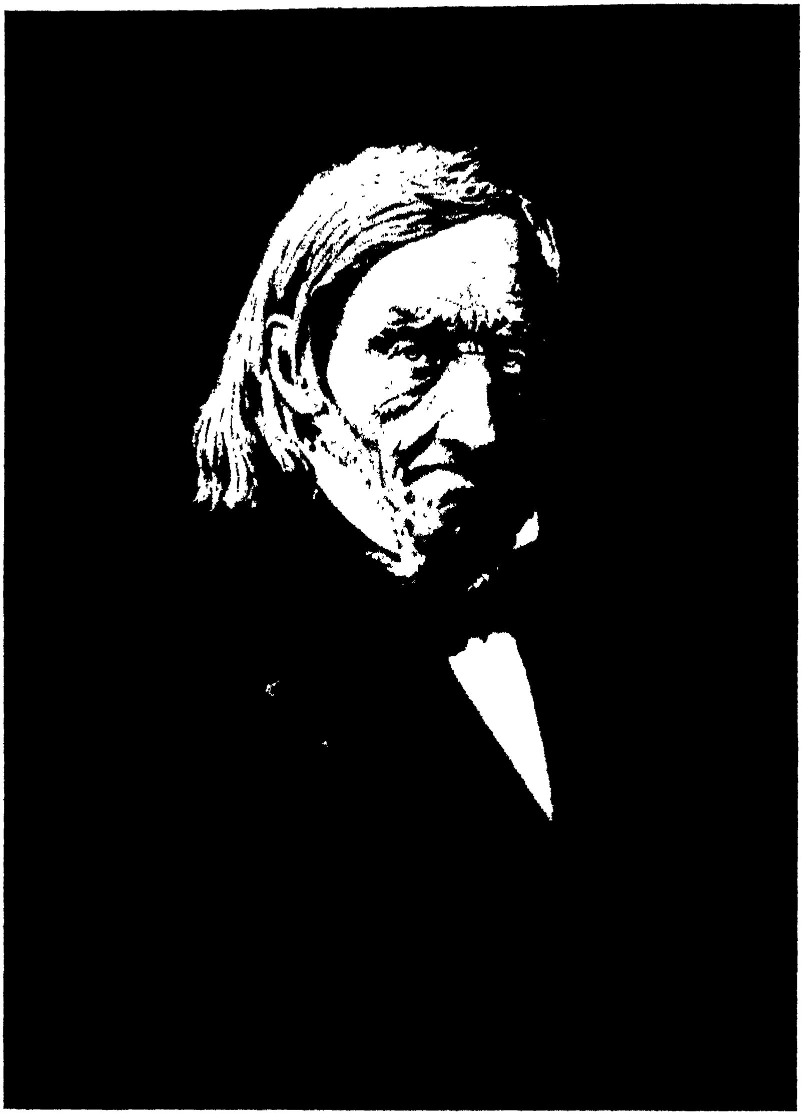
The University of Chicago Press
$3.00 6 x 8⅝; 308 *Chicago*

This book is an interesting one and an important one. It was originally written as a Ph.D. thesis in 1913, and is now being republished. Its rescue from the usual fate of Ph.D. theses is fortunate.

The seventeenth century saw the organization of the earliest of the scientific societies. The present volume is an attempt to show how and why they came into existence, and to estimate their importance in the advancement of earning. Briefly, the author shows how science at the beginning of the century was in the hands of individual scientists, working for the most part in isolation; how, with the rapidly increasing interest in science, and particularly in experiment, little groups of men began meeting to discuss their investigations; and how these groups developed into corporate bodies, publishing their results in their journals. There is a concluding chapter on the universities, showing how, except in Northern Italy and Holland, they were almost as little interested in science at the end of the century as they had been at the beginning.

Whether the author's judgments are in all cases sound is a matter on which opinions will differ. She has, for example, a higher opinion of Francis Bacon than, say, has Augustus de Morgan; and we suspect that she would rate the value to science of original research somewhat higher than would, say, Dr. William Morton Wheeler. Such points as these, however, do not affect the high value of the book.

There is a good bibliography and index.



KARL ERNST VON BAER (1792–1876)

FOUNDER OF THE MODERN SCIENCE OF EMBRYOLOGY; DISCOVERER OF THE MAMMALIAN EGG; CODIFIER OF THE DOCTRINES OF THE GERM-LAYERS AND RECAPITULATION; PIONEER INVESTIGATOR OF THE DEVELOPMENT OF THE VASCULAR SYSTEM

VOL. IV, No. 2 JUNE, 1929

THE QUARTERLY REVIEW of BIOLOGY

THE NEUROFIBRIL HYPOTHESIS

By G. H. PARKER
Zoölogical Laboratory, Harvard University

NERVE cells and reproductive cells share honors in being the most complex cytological elements in the bodies of the higher animals. The cellular nature of the egg and of the spermatozoon was early recognized by the pioneer workers in the field of animal cytology, but it required over half a century of investigation to make clear the true character of the nervous elements. The Cell Theory, proposed by Schleiden and Schwann in 1838–39, was not successfully applied to nervous tissues till 1891. Before that time nerve fibers, ganglion cells, fibrillar material, sense cells and the like afforded a confused mass of elements which were assumed to serve as a basis for nervous organization.

Nerve fibers were apparently first described by Fontana in 1781 (Fig. 1), two years before Monro (1783), in his *Observations on the Structure and Functions of the Nervous System*, called attention to them. They excited the interest of the early workers and were described in much detail by such masters in the use of the microscope as Treviranus (1816) and Ehrenberg (1833, 1836). Ganglion cells were first identified and described in 1833 by Ehrenberg, who published a more elaborate account of these bodies in 1836 (Fig. 2), the year in which Valentin (1836) described numerous nervous organs with their contained ganglion cells.

Five years after the discovery of these cells, that is in 1838, Remak, on the basis of his studies on the sympathetic system, declared that nerve fibers could be traced directly from ganglion cells. This conclusion was supported by Helmholtz (1842) and by Hannover (1843) in their descriptions of the nervous elements of invertebrates. In the work of all these investigators, however, it was not absolutely certain that the fibers found by them in connection with the ganglion cells were really nerve fibers. This uncertainty was removed by the discovery of Koelliker (1844) that in the vertebrates certain medullated fibers, about whose nervous nature there was not the least doubt, could be shown to be in direct continuity with ganglion cells. Thus the connection of ganglion cells and nerve fibers became an established fact.

THE NEURONE THEORY

In 1855 Leydig pointed out in his study of the central nervous organs in spiders that these organs contain, in addition to nerve fibers and ganglion cells, masses of finely fibrillar material to which he gave the general name of punctate substance. Material of this kind was subsequently recognized as a constant ingredient in the gray portions of the spinal cord and of the brain in the higher animals. The interrelations of the punctate substance and particularly of the nerve fibers and the ganglion cells occupied the attention of students in this field of investigation from the middle of the nineteenth century till 1891, when the whole subject was fully reviewed by Koelliker in his presidential address at the Munich meeting of the Anatomische Gesellschaft. This address, which was delivered in May, 1891, was followed in June of that year by Waldeyer's brilliant enunciation of the Neurone Theory, a theory that united in a truly remarkable way a vast array of facts brought to light by the earlier investigators.

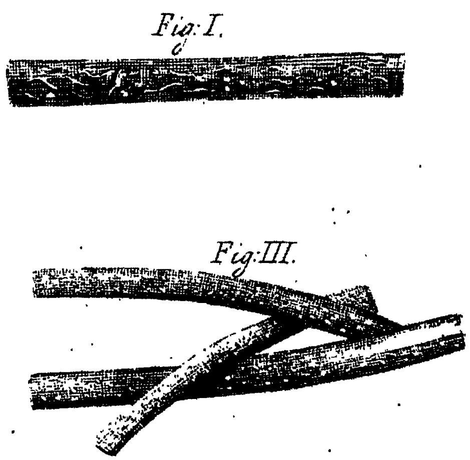


Fig: I.
a
Fig: III.
a

Fig. 1. First Illustrations of Nerve Fibers
Fontana, 1781, p. 204, Tav. IV, Figs. I and III

According to this theory the nervous system is composed of numerous anatomically and genetically interrelated units or neurones each one of which consists ordinarily of three sets of parts: a nerve-cell body, one or more nerve-fiber processes, and numerous finely divided dendritic processes. Such a cell body with its processes constitutes a true nerve cell or neurone and this doctrine was found to be not only in agreement with what was known of the histology of the nervous elements but also with such embryological discoveries as those of His (1886), according to which nerve fibers were shown to be the outgrowths from the bodies of nerve cells. The year 1891 may therefore be looked upon as that in which the cellular interpretation of the nervous elements was first successfully accomplished, for the doctrine of the neurone has been to all intents and purposes universally accepted by the most competent students in the field of general neurology.

THE NEUROFIBRILS

While the discoveries that led to the Neurone Theory were being made, the finer structure of the nervous elements was also being investigated. By such older workers in this field as Treviranus (1816), Ehrenberg (1833, 1836) and Valentin (1836), the contents of nerve fibers and of ganglion cells was believed to be a finely granular material of almost fluid consistency. In 1843 Remak called attention to the fact that in addition to this granular material the larger nerve fibers in the nerve cord of the crayfish possessed an axial bundle of some hundreds of very fine fibrils which ran in parallel courses along the length of the fiber. According to Remak these fibrils were best seen in the fresh condition of the fiber. Soon after a preparation of them had been made they disintegrated and the resulting granular material showed no trace of them. The year after these statements were put forth Remak (1844) published an excellent drawing of this condition in the crayfish (Fig. 3) and also described and figured a ganglion cell (Fig. 4) in whose substance a system of fibrils concentric with the nucleus was clearly shown. No one can read Remak's descriptions or inspect his carefully drawn figures without being convinced that notwithstanding the very imperfect means at his disposal he saw with unusual clearness what subsequent investigators have been led to call neurofibrils.

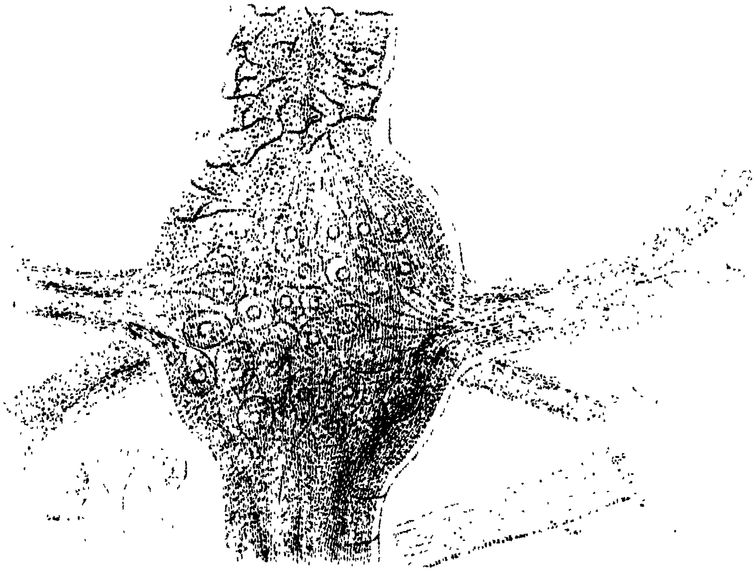


FIG. 2. FIRST ILLUSTRATIONS OF GANGLION CELLS FROM A GANGLION IN THE VENTRAL CHAIN OF THE LEECH

Ehrenberg, 1836, p. 721, Tab. VI, Fig. 7; *7.6*, the whole ganglion; *7.10*, connective nerve fibers; *7.12*, ganglion cells.

Remak's discovery of the neurofibril seems to have excited very little attention among the workers of his time, for in 1847 both Wagner and Bidder published on the structure of nerve fibers and of ganglion cells without intimating that these parts contained anything of a fibrillar nature. Nevertheless Leydig in his *Lehrbuch der Histologie* issued in 1857 referred to Remak's discoveries and described and figured fibrils as component parts of nervous tissue.

WHAT SCHULTZE THOUGHT

It was, however, Max Schultze above all others who raised these structures to a position of first importance. In several papers published in the decade beginning in 1863 this veteran histologist developed his views concerning the nature of neurofibrils. He believed that these bodies could be identified with certainty not only in the axis cylinders of nerve fibers but also in the substance of ganglion cells (Fig. 5). Writing of the large cells in the brain of the Torpedo he stated (1871) that

> It was most convincingly shown here that the large cells removed from the living animal, and prepared in serum, in which they were capable of being easily isolated, possess both in their processes and in their proper substance, an exquisitely delicate fibrillar structure. . . . . Each of the numerous processes of these ganglion cells receives a compound fibril from the cell substance, giving the impression that the

> whole mass of fibrils given off by ganglion cells only traverse it. The nucleus of these cells is seen with a sharply defined outline lying imbedded in the finely granular fibrillated material, but does not appear to stand in any direct connection with the fibrils which cover its external surface. . . . . We may regard such a ganglion cell, from which a peripherally directed nerve fiber proceeds, as representing the source and origin of this axis cylinder, but only in the sense that the fibrils which compose the axis cylinder are collected into a group from the arborescent processes of the cell; and thus the fibrils which are seen traversing the substance of the ganglion cell do not originate in the cell, but only undergo a kind of arrangement in it, and then pass to the axis-cylinder process, or extend into the other branched processes. . . . . The fibrils which emerge in a convergent direction from the cell substance, in order to form the axis cylinder process of the cells, unite, and are often far removed from one another by interfibrillar material. The formation of the proper axis cylinder results from a diminution of the interfibrillar material whilst the fibrils become more closely approximated in their parallel course, so that ultimately only a very small quantity of interfibrillar substance remains. . . . . I consider it, indeed, to be possible that, notwithstanding these observations, axis cylinders exist in which the original fibrillar nature is entirely lost by fusion of the fibrils with each other, and which have thus become homogeneous, but I regard the principle as correct, that the thicker axis cylinders are composed of several primitive fibrils, since these converge at the centric, and for the most part separate from one another at the peripheric extremity. On physiological ground also I maintain the possibility of isolated conduction in these constituent fibrils, even when no trace of interfibrillar substance is present.

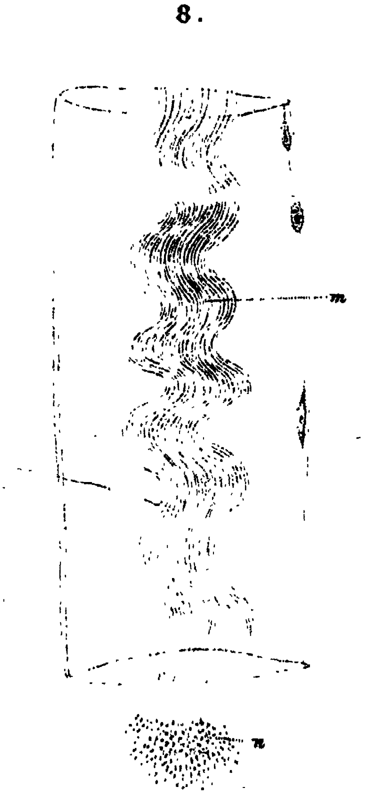


Fig. 3. First Illustration of Neurofibrils from a Nerve Fiber in the Ventral Ganglionic Chain of the Crayfish

Remak, 1844, p. 468, Taf. XII, Fig. 8

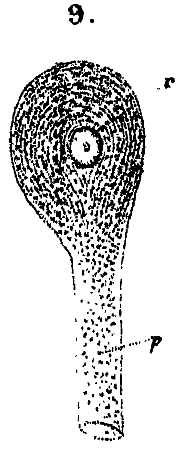


Fig. 4. First Illustration of Neurofibrils from a Ganglion Cell in the Ventral Ganglionic Chain of the Crayfish

Remak, 1844, p. 468, Taf. XII, Fig. 9

It is obvious from these extended quotations that Schultze believed not only in the presence of neurofibrils in ganglion cells and nerve fibers but also that these fibrils form the essential part of the nerve cell and are in fact the structures immediately concerned with that activity which is the most fundamental of all nervous operations, namely, conduction. From this standpoint Schultze may be looked upon as the founder of the Neurofibril Hypothesis. During this period Frommann (1864 a, 1864 b) first stained neurofibrils using silver nitrate and thus added to the certainty with which they could be demonstrated; Deiters (1865) and Beale (1868) also described ganglion cells as bodies in whose substance fibrils could be identified.

Yet notwithstanding these fundamental discoveries and Schultze's clear statement of the Neurofibril Hypothesis these ideas attracted very little attention. Schultze's hypothesis was neither vigorously defended nor vigorously opposed. This apparent indifference was probably due to several circumstances. First of all the Franco-Prussian War, which extended from the summer of 1870 to the following spring, exercised a temporary retardation on all the intellectual activities of the times. Of more immediate importance perhaps than the war so far as the Neurofibril Hypothesis itself was concerned was Schultze's premature death in 1874. Possibly most of all was the absence of reliable methods by which neurofibrils could be clearly and unequivocally demonstrated. To the most expert of the early workers these delicate structures were at best only just within the range of visibility and their identification and investigation were consequently matters of extreme difficulty. Often sought for, they were seldom found and consequently an attitude of suspicion grew up about them that led many to deny their existence. This disbelief in the reality of neurofibrils was a common opinion at that time notwithstanding the fact that a reasonably satisfactory staining method for their demonstration had been devised by Frommann (1864 a) and later a much more satisfactory one by Kupffer (1883). But most of the new methods for the study of nervous tissues, as for instance the Golgi silver impregnation method (1875) and the methylen-blue technique (Ehrlich, 1886), were directed toward the grosser relations of fibers and cells rather than toward the finer structures within these parts. Consequently neurofibrils and their associated problems received relatively scant attention. Thus in the sixth edition of Koelliker's *Handbuch der Gewebelehre* published in 1896 neurofibrils are described as constituent parts of nerve fibers and of ganglion cells, but Koelliker's consideration of them contains nothing of importance that had not already been stated by Schultze in his general account in 1871. The period from the early seventies when Schultze made his mature declarations about neurofibrils till the

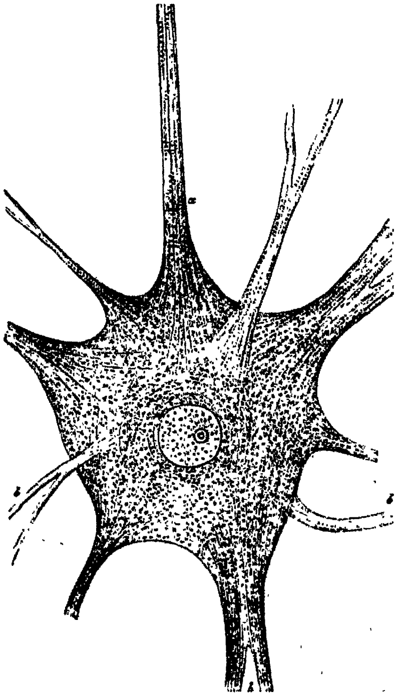


FIG. 5. GANGLION CELL SHOWING NEUROFIBRILS; FROM THE ELECTRIC LOBE IN THE BRAIN OF THE TORPEDO

a, neurite; *b*, dendrite. Schultze, 1871 early nineties was a sterile one so far as neurofibrils were concerned. It was a period in which, as already pointed out, investigators worked on the relations of ganglion cells and nerve fibers rather than on the internal structure of these elements.

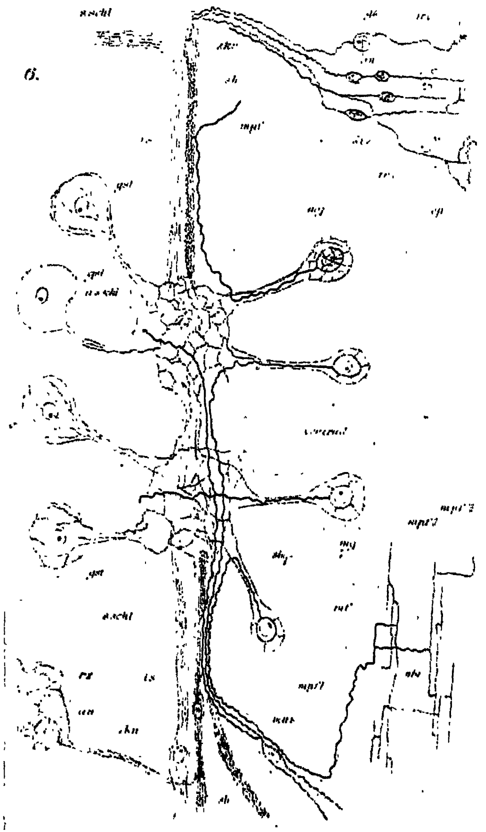


FIG. 6. DIAGRAM OF THE CONDUCTION PATHS ACCORDING TO APÁTHY IN A SOMITE OF THE LEECH

Apáthy, 1897, p. 748, Taf. 32, Fig. 6; *siz*, epithelial sense cells; *sb*, sensory bundle; *dg*, nerve-net in ganglion; *gst* and *mg*, ganglion cells; *mms*, motor bundles; *mf*, muscle fibers.

This period culminated in the nineties in what Bethe (1898 c, p. 96) appropriately called the "Golgi Enthusiasmus."

THE WORK OF APÁTHY

But the Neurofibril Hypothesis even at this time was not without its earnest advocates. In 1889 Apáthy, a brilliant Hungarian histologist working for the most part at the Naples Zoölogical Station, issued a preliminary paper on the direction in which neurology should be reformed and in 1897 he published the first and what proved to be the only part of an extended monograph on the transmitting elements of the nervous system and their relation to the cells. In all of Apáthy's discussion the neurofibril is the fundamental structure. By several new methods of staining, particularly one based on the use of gold chloride, he succeeded in demonstrating neurofibrils with a clarity and distinctness such as had never been approached before. The drawings with which his extended monograph was illustrated showed neurofibrils with such remarkable clearness that many workers believed his figures to be over-enthusiastic attempts in the portrayal of histological details. His preparations, however, were exhibited at a great many scientific meetings at which histologists were present, and those who had the opportunity of examining them were forced to admit that his drawings were in no sense sharper than the details in his preparations. With the clearness of metallic wires neurofibrils could be traced in his preparations through tissue of unusual transparency. Unfortunately the methods by which these preparations had been made were extremely precarious. In the hands of most workers they yielded almost nothing and even Apáthy himself confessed that his own best efforts commonly resulted in complete failure. Nevertheless when the preparations were successful they exhibited neurofibrils as they had never been seen before.

ARE NEUROFIBRILS CONTINUOUS OR NOT?

In such preparations, which were based in the main on material from the leech, the earthworm, and like animals, neurofibrils could be traced according to Apáthy through sense cells, around whose nucleus they commonly formed a network, over nerves and into the central nervous organs (Fig. 6). Here they branched profusely, forming true networks, and as delicate fibrils they entered the bodies of unipolar ganglion cells to form a complicated fibrillar network extending through most of the peripheral protoplasm. From this network branches made their way inward toward the nucleus of the ganglion cell around which was formed a second or inner net, and from this inner net a coarse neurofibril emerged from the ganglion cell, and, after having passed through the central nervous organ again, made its way over a given nerve to a muscle which was thus innervated. In this way continuous neurofibrillar material was believd to extend from a sense cell on the surface of the animal through the central organ to a termination in a distant muscle. In the sensory portion of their courses the neurofibrils were described as fine, in the motor portion coarse. Thus the neurofibril rather than the cell was in Apáthy's opinion the all important element in the organization of the nervous system. Cells in fact were only roadways over which the neurofibrils travelled. These elements, though they started to grow within a given cell, soon spread, according to Apáthy, beyond it, penetrating the substance of other cells as they proceeded toward their final termination.

Apáthy's conception of nervous organization thus laid stress on a continuous neurofibrillar material and relegated nerve cells to a very subordinate position. In both these respects it was in radical opposition to the Neurone Theory. According to this theory nerve cells are the real units of nervous organization. In their early developmental stages as neuroblasts they had been shown to be distinct and separate bodies, whose subsequent union was established through the outgrowth of processes which eventually reached from cell to cell. It was the opinion of most neuronists that the processes from one cell never really fused with those from another but that they were at most simply in contact, a contact which in fact from time to time might even be broken and then reëstablished. Such points of contact, the so-called synapses, were definitely shown to be polarized, in that nerve impulses could pass over them in one direction but not in the other. Thus the advocates of the Neurone Theory emphasized a degree of discontinuity between the nerve cells that was in strong opposition to what Apáthy maintained.

As a result of these differences of opinion a lively debate arose on the question of neural continuity or discontinuity. While this discussion was in progress two new and important methods for the demonstration of nerve cells and neurofibrils were devised. These were Bielschowsky's ammonia-silver method first announced in 1902 and Ramón y Cajal's reduced silver method described one year later. Both methods were modified in a variety of ways and both were so successful as means of demonstrating neurofibrils that these bodies became the objects of active inquiry in many neurological laboratories. The problem that excited the interest of most workers was that already indicated, the degree of continuity or discontinuity between the nervous units. Among those who favored that amount of discontinuity implied in the Neurone Theory were Waldeyer (1891), Retzius (1905), Ramón y Cajal (1908a, 1908b, 1908c), von Lenhossék (1910) and others; the advocates of strict continuity included in addition to Apáthy (1897, 1907a), Bethe (1903), Bielschowsky (1908), Haller (1908), Wolff (1908), and Held (1905a, 1909). It must be admitted that the discussions that took place as a result of these differences of opinion led to no very definite conclusions. Many workers had the opportunity of examining at first hand the remarkable preparations made by Apâthy, but few were able to convince themselves that the preparations gave evidence of the kind of continuity claimed by him. Preparations that had been made in Bielschowsky's laboratory and that seemed entirely convincing to this worker failed to meet Ramón y Cajal's requirements of what a demonstration of continuity should be. Thus in general great uncertainty prevailed. (In a very recent paper Tiegs (1927) has revived the whole discussion by arguing against discontinuity.)

As a possible solution of some of these difficulties it was suggested that the nervous systems of different animals might be differently organized. In the higher forms where the synaptic system prevails discontinuity might be the rule. In the lower forms where the nerve-net is common continuity might obtain. Thus discontinuity might be expected in the nervous systems of one set of animals and continuity in those of another. Such an opinion was expressed by Sherrington (1906, p. 42) and was subsequently elaborated by Parker (1919). To what extent this view is sound is perhaps open to question, for Bozler (1927a) has recently given good reason for believing that the cellular elements in the nerve-net of the jelly fish *Rhizostoma* are quite as disconnected as is assumed for the synaptic system. Should this discovery by Bozler prove well founded, it may result in the complete overthrow of the idea of continuity, for if the synaptic nervous system is composed of discrete units and the same is shown to be true of nerve-nets, continuity as represented by continuous neurofibrillar substance between nerve cells would cease to be tenable. The synaptic system would differ then from the nerve-net only in that the former is polarized in the direction of its conduction and the latter not. In such a case neurofibrils in the nerve-net as well as in the synaptic system would be strictly intracellular structures.

THE DEVELOPMENT OF NEUROFIBRILS

As a result of the introduction of the methods of Bielschowsky and of Ramón y Cajal great additions were made to what had already been known concerning neurofibrils. They were identified in the nerve cells of a wide range of animals from man (Laignel-Lavastine, 1906a) through all the groups of vertebrates (Tello, 1903, 1904; Michailow, 1908; Laignel-Lavastine, 1906b) to mollusks (Legendre, 1906a) and to worms (Ramón y Cajal, 1904; Kowalski, 1908, 1909; Ascoli, 1913; von Szüts, 1914b). Neurofibrillar nets were identified in receptor organs (Van de Velde, 1907), and in motor endplates (Boeke, 1926) and the pathology of neurofibrils was extensively investigated (Ramón y Cajal, 1906b; Marinesco, 1907; Gurewitsch, 1908; Schütz, 1909; Schaffer, 1909; Goodpasture, 1925). Perhaps most important of all was a series of contributions on the developmental history of neurofibrils (Held, 1905b; Brock, 1908, 1909; Fragnito, 1908; Gerini, 1908; Pesker, 1908; MacCurdy, 1909a, 1909b; Cowdry, 1914; Neal, 1915) from which three important conclusions may be drawn: first, neurofibrils develop at a stage much in advance of functional activity either sensory or motor; second, they begin their growth close to the nucleus of the neurone (Cowdry, 1914); and finally, they do not grow beyond the limits of a neurone, that is, they are strictly intracellular (Gerini, 1908). Thus the application of new and improved methods added much to what had been known of these fibrillar bodies.

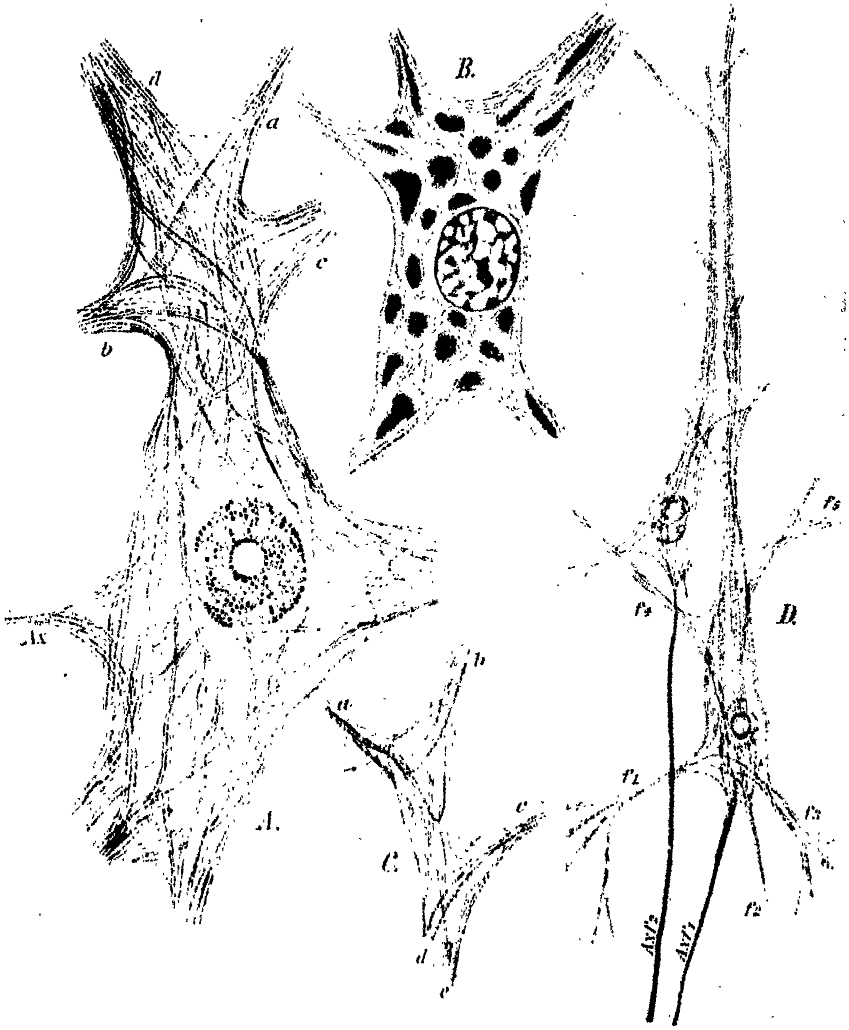


Fig. 7. Ganglion Cells Stained by Bethe's Molybdate Method to Show Neurofibrils

Bethe, 1903, p. 59, Fig. 19; *A*, anterior-horn cell from man; *B*, cell from the nucleus of the facial nerve of the rabbit; *C*, dendrites from a human anterior-horn cell; *D*, human pyramidal cells.

THE WORK OF BETHE

Most intimately associated with the modern investigation of neurofibrils is the work of Bethe, which beginning about three decades ago extended to within the last ten years or so. By novel methods, including the use of such delicate strains as toluidin blue, this indefatigable worker confirmed many of the details of Apáthy's investigations (Bethe, 1898a). According to Bethe (1900) neurofibrils maintain in general independent courses over nerve fibers or through nerve cells, but in certain places true nerve-nets may be present (Fig. 7). In agreement with Apáthy Bethe declared for the continuity of neurofibrillar material, and his views in this respect were criticised in much the same way as those of Apáthy had been (Ramón y Cajal, 1903a, 1906b). Bethe further vigorously advocated Schultze's original declaration that neurofibrils were the transmitting elements in the nervous system.

To this end Bethe offered two interesting pieces of evidence. In the first of these he (1907, 1908) followed a line of experimentation devised somewhat earlier by Jenkins and Carlson (1904). In these tests he attempted to determine the length of time required for a nerve impulse to pass over a given extent of nerve, first in a relaxed state and then in a slightly stretched one. The preparation used was the ventral nerve chain of the leech, and Bethe claimed that the time of transmission remained the same for the lax and for the stretched state. Since the neurofibrils are tortuous in the lax condition and approximately straight in the stretched one it follows that the evidence favored the opinion that conduction is accomplished by these bodies rather than by the neuroplasm or other relatively fluid parts of the fiber which do actually change in length with relaxation and with stretching. Bethe's results, however, were in opposition to those of Jenkins and Carlson (1904) and of Carlson (1905) alone; in the work of these two investigators it was shown that the time of transmission did increase with stretching, a condition which indicated that the transmitting agent was fluid rather than solid. In consequence of this fact as well as of the further one that Bethe's observations were carried out on a piece of central nervous organ and not on a bundle of nerve fibers as those of Jenkins and Carlson were, Bethe's experimental test has not been accepted as crucial.

A second line of evidence introduced by Bethe (1910) turned on the condition presented by the neurofibrils at certain points in the course of medullated nerve fibers. Bethe believed in common with Mann (1898) that at the nodes of Ranvier in these fibers the fluid neuroplasm was completely interrupted and that the only elements that passed through this region were the neurofibrils. Such a state of affairs would of course point to the fibrils as the transmitting parts. But the work of such histologists as Boveri (1886) on the structure of the nodes of Ranvier did not support the opinion of Bethe, nor did this opinion seem tenable to more recent students of the subject (von Lenhossék, 1910). Hence Bethe's second effort to prove that neurofibrils are the conductors of the nervous system failed to be convincing (Ramón y Cajal, 1903a, 1906a).

ARE NEUROFIBRILS ARTEFACTS?

In a cursory survey of the work on neurofibrils covering the ninety years that have elapsed since their discovery it must be evident that students of these structures have come to rely more and more on complicated and intricate methods for the demonstration of these bodies. The discoverer Remak claimed that he saw these fibrils best in fresh cells and fibers. Schultze, their chief advocate, described them from fresh tissue or from that examined in serum. Then came the attempts of Frommann and of Kupffer to stain the fibrils specifically, followed by the brilliant but precarious method of Apáthy, which gave way to the rather intricate but reliable means of demonstration devised by Bielschowsky, Ramón y Cajal, and Bethe. But any one who has worked even with these more recent methods must have been impressed with their precariousness (Legendre, 1906b, 1907a, 1907b). Tello (1922), using the Ramón y Cajal procedure, was able to demonstrate a fibrillar system in connective tissue cells as well as in nerve cells. All workers were familiar with the fact that different preparations made by the same method commonly show great differences in the details of the fibrils and even in the same preparation the fibrils of different parts differ greatly among themselves. This diversity of appearance has been made the subject of critical comment by Clivio (1927), and is the chief basis for that skeptical attitude that many modern workers maintain toward the whole problem. Thus Bayliss (1914) in his *Principles of General Physiology* expressed the opinion that the so-called neurofibrils are pure artefacts produced by the methods employed in the histological preparation of the nervous tissue in which they are seen and that they are in no sense constituents of the living cell. This opinion had also been entertained by Pighini (1908) and Auerbach (1911a, 1911b, 1912). W. H. Lewis and M. R. Lewis (1924, p. 403), both experienced cytologists, reached much the same conclusion. Cowdry (1928, p. 972) on the other hand, after admitting the great uncertainty that is to be attributed to the methods by which neurofibrils have been demonstrated, remarks that these bodies must have some material basis in the cell and that they cannot be due altogether to technique. Somewhat the same opinion as Cowdry's was expressed by Boeke (1926), who admitted the existence of neurofibrils in living tissue but in forms other than those seen in preparations. The ease and quickness with which they disintegrate were emphasized by Marinesco (1914).

A solution for these difficulties is not easily found. The fact that neurofibrils can be demonstrated by a great variety of methods is not conclusive proof, as some have thought, that these bodies are constituents of living cells, for all such methods involve coagulation. Nor does the demonstration of neurofibrils in tissue instantly killed in hot water (Lugaro, 1909) show that the fibrils were present before the killing. In fact no evidence is conclusive on this point except that which can be drawn from living material. What can be demonstrated in the living cell is surely there. Much of the evidence from living cells dates from the time of Remak and Schultze, though fibrils were later identified under the ordinary microscope by Nansen (1887) and under the polarizer by Göthlin (1913). Within the last two years, however, a very important addition to this body of fact has been made by Bozler (1927b).

THE WORK OF BOZLER

This investigator has shown that in the large living nerve cells in the circular nerve band of the jellyfish *Rhizostoma* it is possible to demonstrate with remarkable clearness a system of neurofibrils. These fibrils run lengthwise in the bipolar cells that make up the subepithelial nervous tissue in this creature. When this animal is placed in slightly hypertonic seawater, its nerve cells, in consequence of the general shrinkage of its tissues, shorten and thus throw the bundles of contained neurofibrils into folds (Fig. 8). Under such circumstances the neurofibrils, often partly isolated, can be seen with great clearness in the cells, and yet in this state the tissue is still living, for the jellyfish as a whole continues to pulse and on being returned to ordinary sea water it makes a complete recovery.

Another remarkable fact noted by Bozler (1927b, p. 260) is that after *Rhizos-*

toma has been for some time in hypertonic seawater small hernia-like enlargements appear on the surfaces of its nerve cells (Fig. 9). These sacs are formed in consequence of pressure adjustments and each sac remains attached to its cell by a very narrow neck. Into the cavity of such a sac is squeezed not only some of the fluid neuroplasm from the nerve cell but also portions of its neurofibrils, which fold and bend upon themselves in such a way as to demonstrate in a most conclusive fashion their complete integrity and independence. It would be difficult to devise a more satisfactory demonstration for neurofibrils as real structures in living nerve cells than this is, for the cells are living and the fibrils are observed under these circumstances and without hardening or staining.

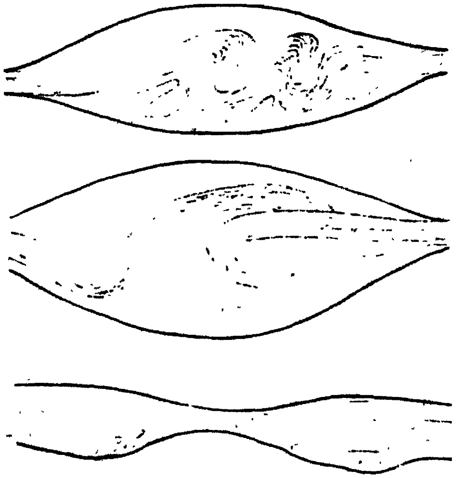


FIG. 8. LIVING NEURITES IN THE JELLYFISH RHIZOSTOMA WHICH HAD BEEN SUBJECTED TO HYPERTONIC SEAWATER; IN CONSEQUENCE OF THIS TREATMENT THE NEUROFIBRILS ARE MUCH FOLDED

Bozler, 1927b, p. 259, Abb. 2

Evidence of this kind points to the correctness of the original observations by Remak and by Schultze and renders it impossible to deny the existence of neurofibrils as constituents of living nerve cells. Incidentally it may be mentioned that although Bozler was the first to call attention in a critical way to the neurofibrils of *Rhizostoma*, these bodies had already been noticed many years earlier in the living tissues of this jellyfish by Hesse (1895).

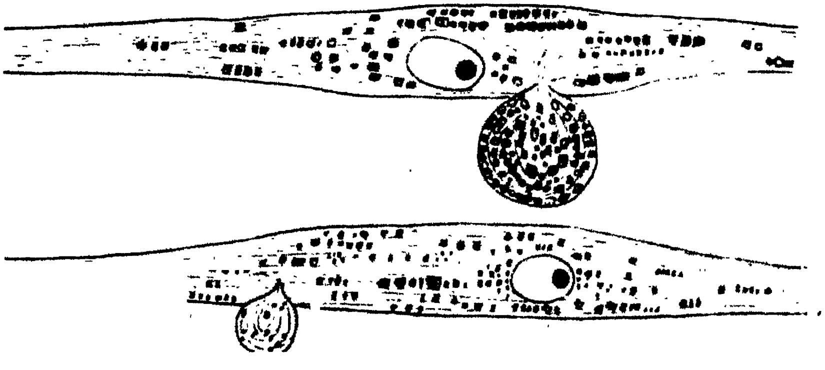


FIG. 9. LIVING BIPOLAR NERVE CELLS FROM THE JELLYFISH RHIZOSTOMA WHICH HAD BEEN SUBJECTED TO HYPERTONIC SEAWATER; AS A RESULT OF THIS TREATMENT THERE HAVE FORMED ON THE CELLS SMALL HERNIA-LIKE ENLARGEMENTS INTO WHICH THE NEUROPLASM AND ITS CONTAINED GLOBULES HAVE FLOWED AND THE NEUROFIBRILS HAVE BENT

Bozler, 1927b, p. 261, Abb. 3

THE STRUCTURE OF NERVE FIBERS

Bozler's work is not only important in indicating what neurofibrils are, but it yields very significant results on the general problem of the physical conditions of the materials contained within ganglion cells and nerve fibers. Aside from minute particles such as mitochondria and the like, the cytoplasm of nerve fibers and ganglion cells contains in the main two materials, neurofibrillar substance and the intervening neuroplasm or interfibrillar material as it is sometimes called. The older cytologists held a variety of opinions concerning the physical properties of these materials. According to Koelliker (1896), Retzius (1889) and others, neurofibrils are filaments of the consistency of a fairly firm gel imbedded in a firm neuroplasm. Thus the whole axis cylinder of a nerve fiber was believed by this school to be relatively resistant, a condition that was supposed to be characteristic of the substance of the nerve cell also. According to another group of workers, represented by such investigators as Leydig (1857) and Nansen (1887), the neuroplasm of cells and fibers was looked upon as a firm material through which the neurofibrils extend as fluid-filled tubules. From this standpoint neurofibrils are not firm bodies but cavities in a matrix of stiff jelly. Finally a third school, composed of many investigators including Kupffer (1883), Boveri (1886) and others, claimed that neurofibrils are relatively tough filaments in a fluid neuroplasm. It is difficult to harmonize the observations of Bozler with the opinions of any of these groups except the third. The formation and filling of hernia-like sacs and the folding of neurofibrils into such sacs, as clearly shown in Bozler's figures, are conditions hardly to be understood except on the assumption of a fluid neuroplasm and a relatively resistant neurofibril. Such an interpretation of the physical condition of these elements is quite in agreement with the observations of Matsumoto (1920) on the movement of small bodies, such as mitochondria, in the neuroplasm of growing axis cylinders and with those of Ingvar (1923) on the shifting of the whole neurofibrillar framework through the neuroplasm of centrifuged nerve cells. These and other like observations show beyond a doubt the correctness of the growing conclusion among neurologists that the neuroplasm of nerve cells and of nerve fibers is a fluid in which relatively firm neurofibrils are suspended.

Although the work on living nerve cells compels us to admit that neurofibrils are real constituents of these bodies, it does not oblige us to accept as such all the structural features that have been ascribed to these fibrils by past workers. Most of these features have been described from specially prepared material, and as already pointed out there is no certainty that they may not be the results of the methods of preparation. Before such features can be accepted, they must be demonstrated in the living cell.

From what is known of neurofibrils in the living state it may be said that they are relatively firm filaments that form axial systems of parallel members in nerve fibers and complicated intermeshing feltworks in cell bodies. They apparently do not divide, nor do they extend beyond the limits of the nerve cell in which they originate. Whether they anastomose and form true networks or not is a question that cannot at present be answered. Such unions were not observed by Bozler (1927a, p. 257) in *Rhizostoma*, where, had they been present, they might easily have been seen. At the moment little more can be said with certainty about the structure of neurofibrils. New discoveries concerning them must await the finding of especially favorable material and the application of novel methods for the study of this material in the living condition.

WHAT IS THE FUNCTION OF NEUROFIBRILS?

In passing from the structural aspect of neurofibrils to their functional side we leave a region in which the light, though dim, is certain for a field of almost complete obscurity. Most of the neurofibrillists, and this includes such vigorous advocates as Apáthy (1899) and Bethe, accepted Max Schultze's dictum that neurofibrils are the transmitting elements of the nervous system. This opinion is almost universal, for only a few workers have expressed other views. Thus von Lenhossék (1910), without, however, denying that neurofibrils may play a part in conduction, regards them as primarily concerned with the mechanics of early development and ascribes to them what might be called a supporting function in the progressive growth of the axis cylinder. That the neurofibrils constitute a purely sustentative system internally bracing the external form of the neurone is the opinion of Koltzoff (1906, 1912), Goldschmidt (1910) and von Szüts (1914a), who in this respect stand out in strong contrast with most other neurofibrillists (Apáthy, 1907b; Bethe, 1913).

It is true that neurofibrils are firmer in texture than the neuroplasm that fills much of the space in the nerve cell, but it is also true, as Bozler, (1927b, p. 258) has pointed out, that this extra firmness is so slight as to be of no real value in forming a skeletal organelle. This conclusion is well supported not only by Bozler's own experimental evidence but also by such observations as those of Ingvar (1923), according to whom the whole fibrillar system of a nerve cell may be broken down by centrifugation without seriously disturbing the form of the cell itself. Thus there seems to be no good reason for assuming that neurofibrils are primarily supporting elements. The neurone maintains its shape chiefly through its outer covering and not in consequence of an inner skeleton.

Having reached this point in his discussion of the function of neurofibrils Bozler (1927b, p. 262) ends by stating that since neurofibrils are not sustentative they must by process of exclusion be conductors. This conclusion would be sound if it could be shown that these two functions exhaust the list of possible neurofibrillar activities. But, it may be asked, are there not other possible functions for neurofibrils than mechanical support and nervous conduction?

As intimated at the beginning of this section there is at present almost no real evidence on which to base a conclusion concerning neurofibrillar activities. At best hypotheses may be framed to which future work may or may not give support. To this category belong the opinions already briefly outlined. They may be designated the conduction hypothesis of Schultze, the histogenetic-sustentative hypothesis of von Lenhossék, and the pure sustentative hypothesis of Koltzoff and Goldschmidt. In this list belongs also the proposition with which this paper closes.

A METABOLIC HYPOTHESIS OF THE NEUROFIBRIL

The life of the neurone is a complex one. In consequence of its function of conducting nerve impulses this type of cell has developed enormously attenuated processes which in the form of nerve fibers penetrate the animal body often for great distances. In man, for instance, some of these fibers have a length of a meter or more, while their diameters may be only five thousandths of a millimeter or about the thickness of a cobweb. A fiber of approximately such a diameter and one meter in length is 200,000 times as long as it is thick. This delicate strand is kept alive throughout its whole extent by its connection with the cell body, whose nucleus is in some way essential to its continued life, for should it be cut through anywhere the part thus separated from the nucleated portion quickly degenerates and dies. This metabolic activity over an enormously attenuated thread is maintained in all nerve cells that they may continue to carry out their very important function of conduction.

The motor fibers of the higher animals transmit certainly two and perhaps three sets of independent influences. First of these is the influence that excites activity in a muscle and that is ordinarily spoken of as the nerve impulse. It passes over these fibers at a relatively high rate, exhibits the all-or-none principle, and is the nervous activity that has been studied for a century or more by workers in the field of nerve-and-muscle physiology. There also pass outward over every motor fiber those influences mentioned in the last paragraph, that are conducive to growth and repair and that are essential for the continued life of every part of the neurone. These metabolic influences emanate from the nucleated portion of the cell and pass to the uttermost ends of the neuronic processes. Finally motor nerves transmit impulses that excite in muscles not momentary activity but that mild continuous contraction, the so-called state of tonus. What these influences are has been scarcely more than guessed at, but that they are different from the other two types is not improbable. They may, however, depend upon a separate innervation from that concerned with ordinary motivity, in which case we are justified in ascribing to any one class of motor fibers not more than two sets of transmitted influences (compare Hardy, 1927).

Two of these three possible sets of influences, the ordinary nerve impulses and the metabolic influences, are recognizable in the sensory neurone, where the independence of these influences is clearly shown by the difference in the direction of their conduction. On the distal stretch of an ordinary sensory neurone in the vertebrates the nerve impulses run toward the central organ, while the metabolic influences run away from it. Hence these two activities must be admitted to be separate.

What parts of the neurone are concerned with these two types of conduction? A final answer to this question cannot be given, but a certain amount of evidence is beginning to appear. It is coming to be a recognized fact, as Hanström has recently noted (1928, p. 481), that the nucleated part of the neurone is its trophic or metabolic center.

From this center, as already pointed out, emanate influences that are essential for the continued life of the whole neurone. This nucleated center is what was designated as the ganglion cell by the older neurologists, and by many of them such cells were supposed to be the seat of the central nervous functions. For years this has been a current opinion, but there is as a matter of fact not the least evidence in favor of it (Nansen, 1887; Bethe, 1904; Parker, 1918). In many instances, such as the bipolar sensory neurones of the lower vertebrates or the bipolar elements in *Rhizostoma*, as recently described by Bozler, the nucleated part of the neurone lies in the line of nervous transmission. But in a number of other cases, as in the unipolar neurones in higher vertebrates and in some invertebrates, the nucleated portion of the neurone is well to one side of the tract of neuronic nervous transmission. In some of these instances the cell body is attached to this tract by only a slender protoplasmic neck. In this type of neurone the courses taken by the nervous impulses and by the metabolic influences are believed on good grounds to be distinctly different. In the ordinary sensory neurones of vertebrates the nerve impulses originate at the peripheral end, make their way centrally over the neurite, and, without entering the body of the cell, pass on to discharge at the central end of the neurone. The metabolic influences on the other hand originate in the region of the nucleus of the cell body, pass down its neck to the tract of nervous transmission where they separate into two streams, one flowing peripherally over the neurite and the other centrally over the central nerve-fiber process.

This conception of the transmission systems within the neurone is favored by the small amount of experimental evidence that has thus far been brought forward. Bethe (1897, p. 629; 1898b) in his study of the nervous system of the crab *Carcinus* showed that the unipolar cell bodies of a group of neurones in the brain of this animal could be removed without disturbing the reflexes of the second antenna, the muscles of which were innervated by these particular neurones. Hence it may be legitimately concluded, as is implied in the preceding consideration, that the cell bodies of many neurones are not traversed by the nerve impulses but that these impulses take a direct course from the receptive to the discharging end of the element concerned.

If, however, we follow the course of the neurofibrillar tracts within such neurones we find them far from agreeing with those of the nerve impulses. The fibrillar tracts occupy the axes of the neurites but at the junction of the neurite with the unipolar cell process they turn into that process and after passing through it, invade the cell body forming extensive whorls around its nucleus. Or, reversing the description, it may be said that the bundles of neurofibrils start from the region of the neuronic nucleus, pass down the unipolar neck of the cell body and spread from that neck distally and proximally over the fibers of the neurone to their terminations.

Thus the course of the neurofibrils does not follow that of the nerve impulses but does duplicate exactly that of the metabolic influences. I conclude therefore that the neurofibrillar system in the neurone is concerned specifically with the distribution of the metabolic influences and not with the conduction of nerve impulses. These influences start in the region of the neuronic nucleus and spread over the lines of neurofibrils throughout the whole neurone. What the metabolic influences are it is impossible at present to say. It seems hardly reasonable to think of them as streams of material in the nature of a hormone, emanating from the region of the nucleus and percolating throughout the neurone. Such a passage of material might however occur over interfacial boundaries as already suggested for the true nerve impulse by Brinkman and Szent-Györgyi (1923). Or they may be chains of ionic readjustment such as have been proposed as an explanation of the nerve impulse. But however we consider them, the hypothesis here put forward assumes that they are what the neurofibrils transmit. This hypothesis further assumes that the neurofibrils are not concerned with the transmission of the nerve impulse, as asserted by Schultze and advocated by Apáthy and Bethe, nor with the mechanical support of the neurone as maintained by Koltzoff and Goldschmidt and in a qualified way by von Lenhossék.

If nerve impulses are not transmitted by neurofibrils what part of the neurone does transmit them? Von Lenhossék (1910) was probably correct in declaring that no specific part of such a cell can be singled out for this special activity. The transmission of nerve impulses, according to him, is rather a function of the neurone as a whole, than of any of its parts. And yet certain of these parts are probably more intimately concerned with this operation than others are. The growing belief as to the nature of the nerve impulse is that it is a progressive wave of ionic readjustment in some membranous layer of the neurone (Lillie, 1923). Where this layer is located is not easily determined, but that it is about the surface of the neurone is much more probable than that it is buried in its depths. The periphery of the axis cylinder is a much more probable location than the core of that structure. It is well known that if we estimate the metabolism of nerve fibers by the carbon dioxide they give out and designate the amount of this gas discharged by a given quantity of quiescent fiber in a given time as 100 per cent, the increase due to the passage of nerve impulses in the active state of the fiber is only some 15 per cent (Parker, 1928). These relations are not inconsistent with the belief that the core of the fiber is concerned with maintaining a state of responsiveness on the surface by which the fiber on stimulation is enabled to transmit impulses and to recover from the effects of such transmission. From this standpoint the core of the axis cylinder is believed to be concerned chiefly with metabolic activities, the periphery with transmission. While this statement is a pure assumption there are no facts so far as I am aware that prevent its acceptance.

The hypothesis that neurofibrils are the parts of the neurone especially concerned with the metabolism of its more distant parts is not only supported by the distribution of these fibrils within the neurone but also by their course of development. It will be remembered that two important facts stand out in the developmental history of the neurofibrils: first, that their initial appearance is in close proximity to the neuronic nucleus and, second, that they develop while the neuroblast is gradually changing into a neurone and some time before nervous functional activity has appeared. Both these facts are without special meaning if we assume neurofibrils to be conductors of nerve impulses, but both are significant if we believe the fibrils to be concerned with metabolic influences, for these influences emanate from the nucleus and must be of first importance in the early stages of neuronic growth and before nervous activity has begun. Thus the little that is known of neurofibrillar development favors the hypothesis set forth in this paper rather than that of nervous conduction.

The idea that the neurofibrillar system of the nerve cell is a part of the metabolic outfit of the neurone is avowedly hypothetical and yet as an hypothesis it meets at present more of the known facts about the neurone than the hypotheses of nervous conduction or of support appear to do. Hence comes the justification of its presentation, in full understanding that its worth will be determined as our knowledge of the neurone increases.

POSTSCRIPT

In addition to the fibrillar systems in nerve cells there are two other sets of fibrils that call for some consideration. These are the fibrils in the cells of many ciliated epithelia and in the cells of certain protozoans. In both instances these systems have been interpreted as means of controlling the beat of the cilia or other like parts on the given cells.

The fibrillar system in ciliated epithelia has been recently studied with much care by Grave and Schmitt (1925), who have shown, for instance, that in cells from the foot of the mollusk *Lampsilis* a fan-shaped system of converging fibrils occurs, the spread ends of which are in contact with the basal bodies of the cilia and the converging ends of which terminate in the deeper part of the cell close to the nucleus (Fig. 10). These fibrils, which were long ago described in other similar cells, are believed by Grave and Schmitt to be the means of regulating the metachronous beat of the cilia. But this beat passes over the whole ciliary field without reference to cell limits and it is therefore difficult to understand how such a distinctly cellular mechanism as this is could serve as a regulator of such an activity. On the other hand a comparison between the nerve cell with its neurofibrillar system leading from near its nucleus to its peripheral parts and the ciliated cell with a fibrillar system that also starts from close to its nucleus and extends to the basal ends of the cilia is highly suggestive. It is quite possible, judging from the connections shown in the ciliated cell, that its fibrillar system is in reality a counterpart of that already described for the nerve cell. The nucleus of the ciliated cell is without doubt its metabolic center and the cilia are obviously the parts that would call most heavily on the metabolic resources of the cell. Are not the fibrils, then, that lead from the region of the nucleus to the cilia the most probable parts to be concerned with this transfer of resources? With this view in mind a comparison between them and the neurofibrils of nerve cells seems reasonable.

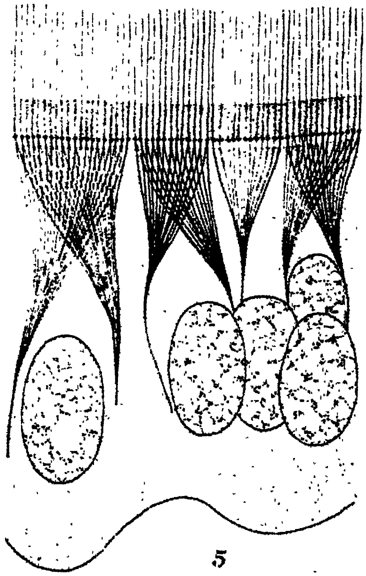


FIG. 10. CILIATED EPITHELIUM FROM THE FOOT OF THE MOLLUSK LAMPSILIS SHOWING FAN-SHAPED BUNDLES OF FIBRILS EXTENDING FROM NEAR THE NUCLEUS OF THE CELL TO THE BASES OF THE CILIA

Grave and Schmitt, 1925, p. 513, Fig. 5

A second system of fibrils that has recently attracted the interest of investigators is that contained in the cell bodies of certain protozoans. These fibrils have been claimed to constitute what has been called a neuromotor system and the function ascribed to them has been the conductive activities in the control of the cilia, commonly the specialized cilia, of these protozoan cells. From this standpoint they were studied first by Sharp (1914) and later by Yocom (1918), Kofoid and Swezy (1919), Taylor (1920), McDonald (1922), Rees (1921, 1922), and Visscher (1927). All these workers have interpreted the fibrils as parts of a neuromotor system. It has, however, been pointed out that they may serve as a purely supporting mechanism. In *Euplotes* (Yocom, 1918; Taylor, 1920) *Trichomitus* (Kofoid and Swezy, 1919) and *Paramecium* (Rees, 1921, 1922) the systems from the cilia concentrate on a center that is in close proximity to the nucleus, a condition that favors the extension of the hypothesis advanced in this paper for the fibrils in nerve cells and in ciliated cells to those in the protozoan cell. It must be remembered, however, that in two protozoans, *Diplodinum* (Sharp, 1914) and *Balantidium* (McDonald, 1922), systems of fibrils have been described concentrating on a so-called motorium not located near the nucleus. It is, however, possible that these systems may be something other than those described for *Euplotes*, *Trichomitus*, and *Paramecium*, in which the nuclear relations are most obvious. It would be difficult to imagine a system better placed for the transfer of metabolic influences from the nucleus to the cilia than that described by Rees for *Paramecium* (Fig. 11), and when it is remembered that, as Jennings and Jamieson (1902) long ago showed, fragments of *Paramecium* continue to exhibit essentially normal ciliary activity for many hours after they have been prepared, it would seem likely that the fibrillar system in this protozoan was more concerned with some such function as that ascribed to it in the present paper than with the immediate control of the ciliary beat.

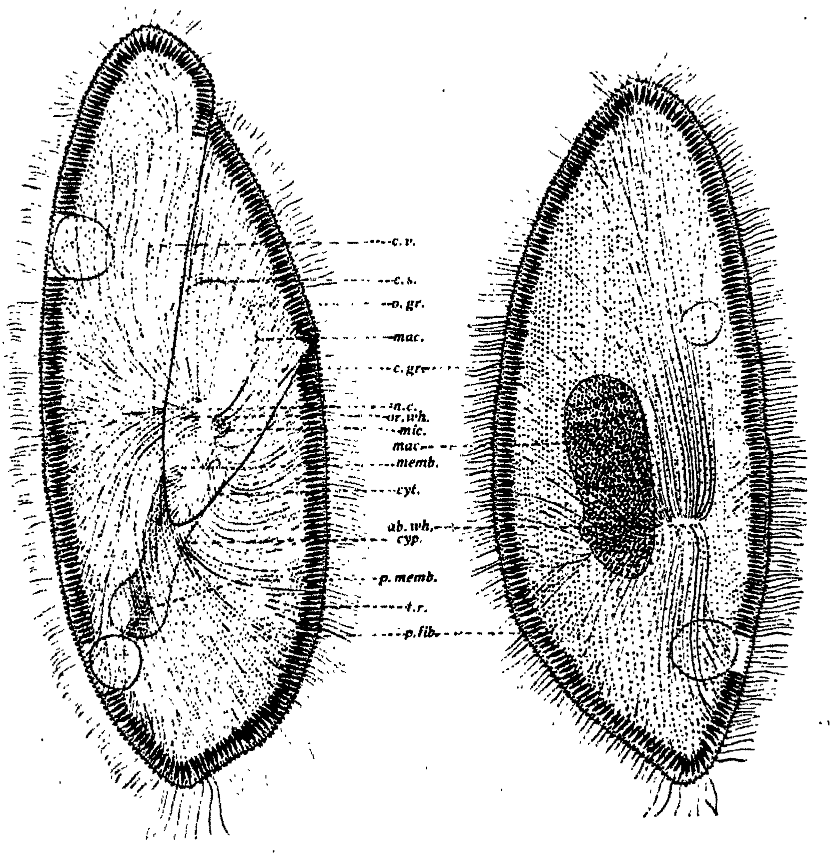


FIG. 1. FIG. 2.

FIG. 11. SEMIDIAGRAMMATIC SKETCH OF THE SYSTEM OF FIBRILS IN PARAMECIUM

Rees, 1921, p. 465; *mac*, macronucleus, toward which the fibrils concentrate on both the oral (Fig. 1) and the aboral side (Fig. 2) of the protozoan.

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A CENTURY OF STUDY UPON THE DEVELOPMENT OF THE EUTHERIAN VENA CAVA INFERIOR

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ONE hundred years ago, Karl Ernst von Baer published the first part of his monumental work: *Ueber Entwickelungsgeschichte der Thiere; Beobachtung und Reflexion.* For many structures this great work serves as the classic foundation of modern embryological study, and of the veins this might especially be said. It would seem fitting and proper, after a century has elapsed, that we pause to take stock of what has been accomplished. Concerning the veins we may say this: the time is ripe for an assessment of the literature, with a view to determining what it contains of permanent value. The majority of opinions entertained by former observers, especially with regard to the vena cava inferior, obviously cannot continue indefinitely to receive mention by those who essay to present historical introductions along with their supposedly new opinions apropos of that vein. Out of respect for past investigators and for the convenience of future readers, it is desirable that the elimination of what is thought to be irrelevant be carried out justly, and that credit for discovery be bestowed where it belongs. So far as the inferior vena cava is concerned, it must be admitted that our progress has not been such that we are able to look back from the goal of ultimate truth and presume to say who has deviated least from the path leading to it. For just ever been except, perhaps, during the year 1888.

Modern methods and appliances have, however, advanced to such an extent that the problems of the veins do at least lend themselves to solution. Technique has been evolved which might conceivably enable us to produce accounts complete enough for all practical purposes and graphic expression. On the purely material side there is hope. But, the trend of Anatomy being what it is, well may we wonder whether the lure of Physiology will leave among us those with training and fortitude sufficient to the adequate disposal of the problems of venous development. Among many writers of textbooks of Embryology, to say nothing of the students of that subject, there exists a feeling of genuine aversion towards further progress in the study of veins if that is to involve greater intricacy and detail than existing accounts would indicate. Doubtless this difficulty with regard to the veins might be overcome if we were to produce a really complete account, place it safely in our archives, then prescribe for the unwilling student a diluted dose of venous embryology.

Whether we are in the throes of the final act, or whether the year 1928 merely sees us entering, with misgivings, into a second century of work upon venous development, it is well at this auspicious time to segregate and to summarize a ing the truth of which we may feel relatively sure.

PERIODS IN THE STUDY OF THE VASCULAR SYSTEM

Definite eras through which the study of the vascular system has passed may be significantly associated with certain vogues of technique. The great classical work upon the development of the vascular system may be said to have been ushered in with the nineteenth century. The previous century had brought about advances in the study of comparative anatomy. Cuvier and Meckel were the leaders of such study in the early part of the nineteenth century. Of the study of the embryology of the vascular system, von Baer and Rathke were the great pioneers. They, like their predecessors, depended largely upon the direct observation of the living embryo, relatively fresh material, or the dissection of preserved material. Wolff, Malpighi, Haller, Hunter, Spallanzani, Döllinger, Pander, Gruithuisen, Kaltenbrunner, and others had examined and figured the living blastoderms, studied the vascularization of the embryonic membranes, the developing vessels in transparent portions of larval amphibia and various fishes, the more superficial intraembryonic vessels, circulation in the external gills, and the heart; the latter structure was a favorite object for early investigations.

An extensive review of the early nineteenth century work upon the origin of endothelium is given by Allen Thomson (1832). Near the year 1815 there was controversy over this subject, perhaps less intense but equally intelligent as that which subsided in 1915. Among the names recorded in Thomson's discussion are those of the most eminent anatomists of that time.

The era of von Baer and Rathke (which I shall arbitrarily term the "classical period") is characterized by figures in which the vessels are shown in their original relations to accurately drawn neighboring structures—veritable direct illustrations of embryonic bodies, parts, or dissections. This era extended to about the year 1840. Inadequate microscopical equipment and a shortage of closely graded material offset to an extent the advantages of skill and of the remarkable capacity for accurate observation possessed by these great investigators.

Then followed some forty years of relative inactivity. There is no better way of determining the situation in anatomy at that time than to consult the indices of the *Archiv für Anatomie und Physiologie* of the period. Anatomists had turned to physiology and to chemistry. The period was characterized by what Professor E. G. Conklin (*Science*, vol. 68, no. 1768) has most aptly called 'frantic physiology.' But with the popularization of the serial section and later the wax reconstruction there came, for the embryology of the vascular system, a renaissance in which His and Hochstetter may be regarded as the great leaders. The period is preeminently that of figures and diagrams of models of the larger vascular trunks removed from their topographical relationships with other structures. The method lent itself to the study of deep vessels which had never been seen by direct observation. The twentieth century, that of recent study, has seen a refinement of the technique of sectioning and reconstruction, as well as a revival of the injection method. The latter had been used occasionally upon foetal and embryonic material by such early workers as John Hunter, Huschke, and von Baer.

Modern investigators have succeeded in rediscovering a number of facts recorded in the classical accounts long since forgotten; and they have been not entirely reluctant to accept discoverers' credit for the restatement of that which had already been thought to be true. Recent investigators have been content to restate the reviews written toward the end of the nineteenth century. American observers especially, for want of libraries containing the earlier literature, have often had to give their assent to previous reviews and have often merely cited those references which had obviously not been available for direct perusal. Thus it is that certain misconceptions have come to be regarded as historical facts. Our perspective for the study of veins is incomparably worse than it is for most embryological study. Modern investigators have failed particularly to appreciate the amount of information possessed by von Baer and by Rathke with regard to embryonic capillary plexuses generally, and the development of the cranial vessels and dural sinuses specifically. (Consult especially Rathke (1839, p. 111) on the direct protracted observation of the capillaries of the brain wall of the living snake embryo and his studies of the venous sinuses of the head.)

THE WORK OF KERSCHNER

In the present account it will be possible to treat of only a few details of early work upon the development of veins of the dorsal body wall. In any serious attempt to determine the proper use of the terms *Vena cava inferior* and *V. cardinalis posterior*, it is necessary to consider the historical relationships of these two terms. Certain value was evidently attached by Hochstetter to the historical account given by Kerschner (1888-a). Many valuable references cited by Kerschner appear in the discussion by Hochstetter (1893), who concurs (*ibid.*, p. 611) with Kerschner (1888-a, p. 812) that the work of Stark (1835) probably influenced Rathke (1838) to abandon certain notions of the vena cava which he had entertained in 1830. Lewis (1902) depended in part upon Hochstetter's (1893) review. Huntington and McClure (1920) refer to the work of Hochstetter and Rathke as being fully appreciated by them. Butler (1927, p. 269) shares the view of Kerschner concerning the influence of Stark upon Rathke. Sabin's (1915) review of the literature of vena cava is manifestly based upon Kerschner, whose statement of the problem as a whole is accepted by Sabin. Butler's review (1927) reiterates many of the statements of Hochstetter (1893) and several which Sabin had based upon Kerschner, and recommends Kerschner's review as a source of valuable information. There is thus a definite tendency to depend upon Kerschner for our perspective. If we accept the statements of that author, then the personality of Stark bulks large in the history of our knowledge of the vena cava. It can be shown, however, that many of the statements of Kerschner are not to be taken seriously. Hochstetter (1888-a) has demonstrated this to an extent. In turn, Sabin's presentation of Kerschner's views is in some ways unreliable, and is particularly misleading, insofar as it gives the impression that Kerschner offered a correct interpretation of the inferior vena cava. For the author who attempts it, the task of unravelling all this confusion is not a profitable one, nor would a complete survey of the historical facts be the most pleasant subject-matter possible for the consideration of those persons who cannot endure the spectacle of authors expressing opposite opinions enthusiastically. Yet we may certainly say that if distorted or inadequate reviews have been thought worth the printing, then additional effort is warranted in the elimination of confusion which these reviews have occasioned, and those authors who have contributed to the confusion should be the last to complain.

I propose to review first the accounts of Kerschner (1888-a and -b) in relation to the work of Hochstetter (1887, 1888-a, -b, 1893, and 1902); in relation to the work of Rathke and Stark; and in relation to recent work. The contributions of the early authors may then be considered in relation to each other. The announced purpose of Kerschner's first article (1888-a) on the morphology of the V. cava inferior is that of determining an anatomical and embryological basis for interpreting certain venous anomalies. The greater part of the discussion is occupied with refuting the conclusions of Hochstetter (1887).

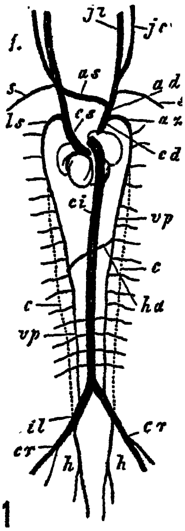
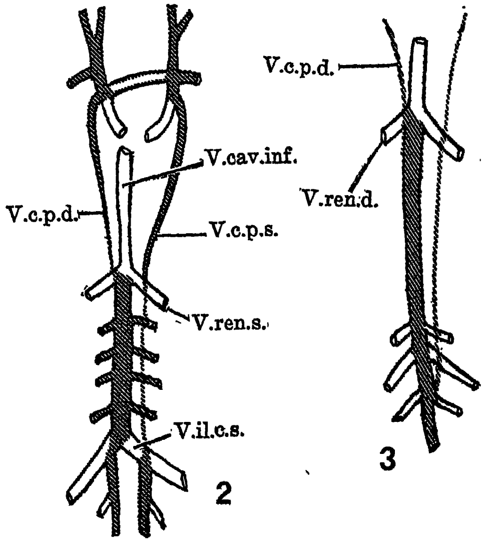


FIG. 1. SCHEMA TO REPRESENT THE DEVELOPMENT OF THE SYSTEM OF SUPERIOR AND INFERIOR CAVAL VEINS

(From figure 276, p. 404, Kölliker's *Grundriss der Entw. des Menschen u. der höheren Tiere* (1884).) *c*, "obliterated middle portion of the cardinal veins"; *vp*, "newly developed 'posterior vertebral' veins, forming new portions of the azygos and hemiazygos lines and receiving lumbar and intercostal veins." For the explanation of the remainder of the labelling consult the original. The figure is obviously based upon Rathke's description (1838).

THE WORK OF HOCHSTETTER

For a period of some fifty years prior to the work just mentioned, writers of embryological text books had generally accepted the notion of Rathke (1838) that the azygos veins (largely) and the postrenal V. cava (entirely) are new formations independent of the cardinal veins. Diagrams similar to those of Gegenbaur (1870), Henle-Krause (1876), and Kölliker (1884) served to explain the developmental process (consult my figure 1). Hochstetter's (1887-a) diagrams showed V. azygos and V. cava inferior as cardinal derivatives. Elaborations of these latter figures are



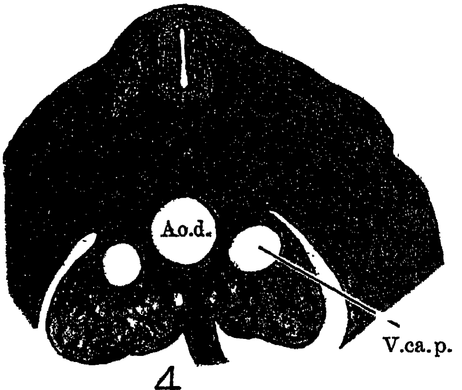
FIGS. 2 AND 3. DIAGRAMS TO REPRESENT THE FORMATION OF THE POSTRENAL V. CAVA IN MAN (2), AND IN THE RABBIT (3)

(From Hochstetter 1887, p. 518.) According to this schema, the V. cava inferior and the azygos and hemiazygos veins are directly derived from posterior cardinal veins. It was from these diagrams that Hertwig executed his figures on p. 537 of his *Entwicklungsgeschichte des Menschen und der Thiere*, 5te Aufl. The latter diagrams are copied in many recent textbooks. They are often represented as being derived from the figures of Hochstetter. Not only are they inadequate to illustrate Hochstetter's views, but they fail to portray conditions even remotely resembling those in any mammal. Minot (1898) called attention to their inadequacy.

those employed in most of the recent embryological text books (consult my figures 2 and 3). Kerschner (1888-a) contended that these latter diagrams of Hochstetter were incorrect, and that even if they were correct, the notion which they illustrate was not original with Hochstetter, but that they represent a theory of venous development expounded by Rathke (1830-a); that Rathke had abandoned this theory, influenced probably by the work of Stark (1835). Kerschner pointed out (as noted by Sabin) that the V. cava lies medial to the kidney, whereas the cardinal vein of Rathke lies lateral to it. Hochstetter replied (1888-a) to this criticism as follows:

> that his view was neither a confirmation of the earlier (1830-a) nor the later (1838) view of Rathke; that Rathke (1830) had merely followed the current practice of designating as "hintere Hohlvenen" two large posterior vessels in plain view for direct observation (this being the means of study at Rathke's disposal); that these "hintere Hohlvenen" are "was wir heute *hintere Cardinalvenen* nennen;" that the right "hintere Hohlvene" of Rathke (1830) in its totality could not possibly become V. cava; that Kerschner was oblivious to the possibility (as supposed by Hochstetter) that Rathke could not have seen the posterior cardinal veins in their mesonephric segments; that whereas Rathke (1830-a) describes "zwei einander höchst ähnliche Gefässe 'deren jedes an der äusseren Seite der beiden falschen Nieren,' von hinten nach vorn verlauft," the cardinal veins (according to Hochstetter, 1888-a, p. 871) "liegen nun bei Säugetierembryonen nie an der äusseren Seite der Urnieren —" but dorsomedial to it from the time of their first appearance; that the mesonephric sections of these vessels could therefore not have been observed by Rathke, who consequently "die Hohlvenenentwickelung zweimal in verschiedener Weise unrichtig beschrieben hat;" that the mammalian postrenal V. cava inferior lies upon the dorsomedial border of the mesonephros throughout the existence of that organ and that its position at all times "vollständig mit der rechten hinteren Cardinalvenen übereinstimmt;" that Kerschner had merely consulted a certain amount of literature and had given play to his imagination. It is from the store of knowledge of V. cava possessed by Hochstetter in 1887 (represented usually by Hertwig's diagrams) that most modern text books of embryology have acquired the material for their accounts of that vessel.

We need not enter into the details of Kerschner's (1888-b) reply to Hochstetter, but preferably we may note the advance made by the latter observer (1888-b) in his article dealing with the influence of the permanent kidney upon the development of the veins. This appeared simultaneously with Kerschner's reply. From this article (Hochstetter, 1888-b) one learns that the series of embryos which he had previously (1887) studied did not afford stages of development exhibiting a venous "island" in which the permanent kidney can be seen to be encircled by veins. For the history of the subject this is an admission, the importance of which deserves emphasis. Hochstetter's accounts (1887 and 1888-b) present differences practically as great as those of the accounts by Rathke (1830-a and 1838). His statement (1888-a), already quoted, to the effect that the posterior cardinal is never found on the dorsolateral border of the mammalian mesonephros can in no way be harmonized with his description of the original posterior cardinal line as given in his later account (1888-b). In this connection consult my figure 6. In younger stages he had apparently noted conditions similar to those seen in figure 4. In older stages he had probably noted conditions seen in my figure 5. His greatest error was to suppose (1888-a) that the dorsal aorta is a reliable landmark by which to establish the identities of vessels lateral to its postrenal segment in two somewhat separated stages of development. When he had acquired sufficient material upon which to make a more complete study (1888-b), he found conditions similar to those in figure 6. On pages 939 and 940 of the latter account he stated that the more lateral vessel involved in this "island-formation" (consult figures



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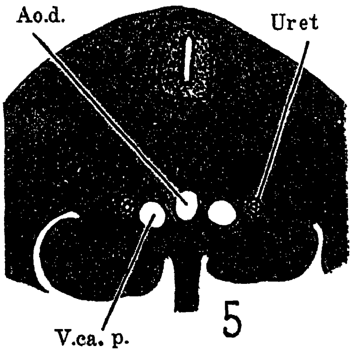

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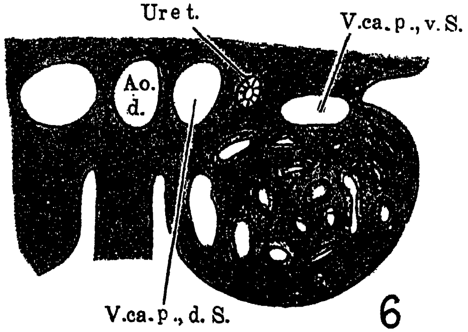

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Fig. 4. Cross-Section through the Mesonephroi of a 13-day Rabbit Embryo Showing Correctly the Original Relation of Posterior Cardinal Vein to Mesonephros

(After Hochstetter, 1888-b, p. 939, figure 1.) *Ao*, aorta, *V.ca.p.*, vena cardinalis posterior.

Fig. 5. Cross-Section through the Postrenal Mesonephric Segment of the Inferior V. Cava of a 15-day Rabbit Embryo

(From Hochstetter, 1888-b.) The Anlage of V. cava of the region is labelled *V.ca.p.* (V. cardinalis posterior). In 1887, Hochstetter erroneously considered such vessels as *V.ca.p.* in figures 4 and 5 to be identical structures. *Uret.*, ureter.

Fig. 6. Cross-Section through the Mid-lumbar Region of a Rabbit Embryo, Second Half of the Fourteenth Day

(Copied from Hochstetter, 1893, *Tafel* 22, figure 14.) This shows Hochstetter's later interpretation of posterior cardinal vein (*V.ca.p., v.s.*) in relation to a newly-established 'Collateralvenenbahn' (*V.ca.p., d.s.*) which forms the mid-lumbar portion of V. cava. These two vessels are described as ventral and dorsal "Schenkeln" of a "Cardinalveneninsel." The "ventral Schenkel" represents the *V.ca.p.* of figure 4. The "dorsal Schenkel" really represents the *V.ca.p.* of figure 5.

6 and 7) was a segment of the original posterior cardinal vein which had been pushed aside and compressed dorso-ventrally by the "migrating" kidney; that this pressure had not only displaced the posterior cardinal, but had interfered with the flow of blood in it; that as a consequence there developed (in the rabbit) a new vein taking exit from the posterior cardinal at the level of the caudal end of the kidney and reentering that vessel at the cranial end of the kidney; that the original cardinal line so involved rapidly degenerated, while the new vessel, designated by Hochstetter as a new "collateral Venenbahn" rapidly increased in size to form postrenal vena cava of the region. Summarizing this, he stated:

> Es hat sich also in Urnierabschnitt der hinteren Cardinalvene jederseits eine Insel gebildet, in welche die Anlage der bleibenden Niere gewissermassen hineingesteckt erscheint. Der dorsal Schenkel dieser Insel nimmt nun die gleich Lage zur Aorta ein wie früher die Cardinalvene *selbst*.

The term "periureteric venous ring of Hochstetter" as employed by recent authors is a misonomer. He used no such term. The statement of the fundamental problem (by Kerschner and by Sabin) as being involved in the question whether a vessel lateral to the kidney could ever become vena cava might imply this: that authors who claimed vena cava to be of posterior cardinal origin must have believed vena cava to form lateral to the kidney. Neither in his earlier nor his later work did Hochstetter express such a belief.

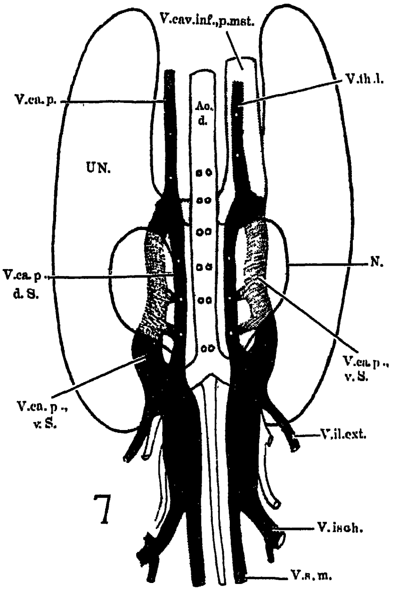


FIG. 7. MESONEPHROS, KIDNEY, AORTA, AND V. CAVA INFERIOR OF A RABBIT EMBRYO AT THE MIDDLE OF THE 14TH DAY ILLUSTRATING THE "CARDINALVENENINSEL" IN RELATION TO THE URETER

(Modified from Hochstetter, figure 19, *Tafel* 23, 1893.) On the left side of the figure, the venous path regarded by Hochstetter as being derived from the original posterior cardinal line is shaded by diagonal lines. The new "dorsal Schenkel" of the "Insel" is shown in solid black. The present writer has taken liberty to modify the right side of the figure to the extent of showing the prerenal *V.ca.p.* of the original as a new formation labelled *V. thl.* according to a suggested usage (Reagan, 1927-b). The parts of the "Cardinalveneninsel" are labelled in accordance with the usage in the preceding figure. *A.i.e.* and *V.i.e.*, "internal iliac" vessels. *V.i.*, ischiadic vein. *A.s.m.* and *V.s.m.*, medial sacral vessels. *U.N.*, mesonephros. *N.*, metanephros and ureter.

Hochstetter has remained reluctant to apply a new and specific embryological term to the above-described "collateral Venenbahn" which contributes to postrenal vena cava. Much less has he seen fit to apply to it a term dissociated from the term *cardinal vein*. The nearest approach to a specific embryological term for it, in Hochstetter's usage, is "dorsal Schenkel" of the "Cardinalveneninsel." On the contrary he was willing to apply to the "ventral Schenkel" of the "Cardinalveneninsel" a specific term not involving the concept of "cardinal." I

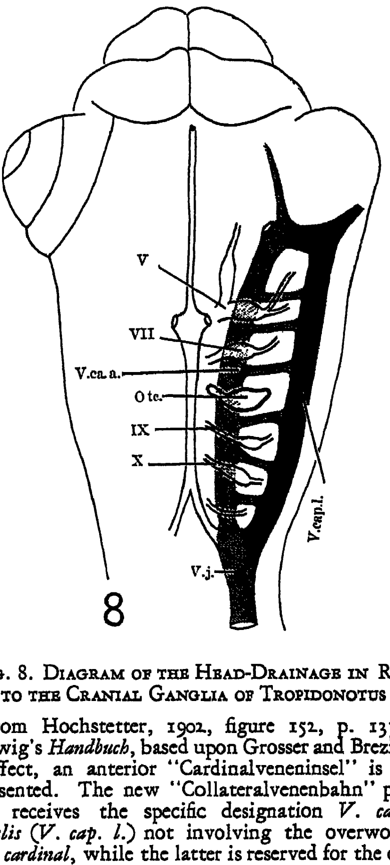
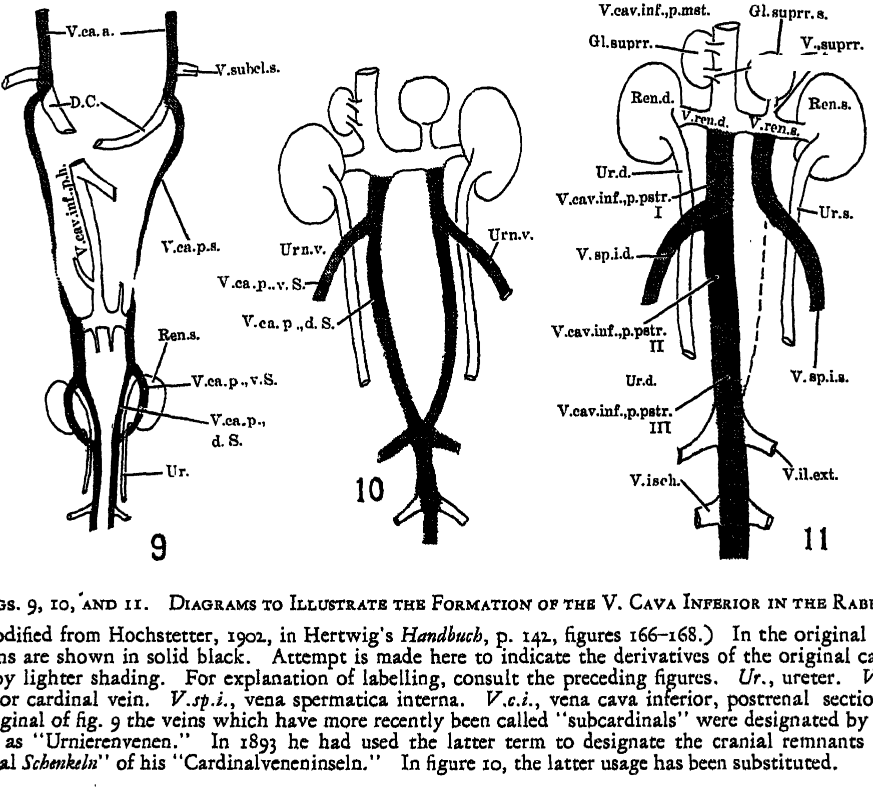


FIG. 8. DIAGRAM OF THE HEAD-DRAINAGE IN RELATION TO THE CRANIAL GANGLIA OF TROPIDONOTUS

(From Hochstetter, 1902, figure 152, p. 133 in Hertwig's *Handbuch*, based upon Grosser and Brezina.) In effect, an anterior "Cardinalveneninsel" is here represented. The new "Collateralvenenbahn" properly receives the specific designation *V. capitis lateralis* (*V. cap. l.*) not involving the overworked term *cardinal*, while the latter is reserved for the original "Schenkel" of the "Insel." The cranial ganglia are indicated by Roman numerals. *Otc.*, otocyst. *v.j.*, vena jugularis.

refer to his term "Urnierenvene" which he applied (1893) to a derivative of the original cardinal vein. In general, this usage was carried out in Hochstetter's account in 1902. In the latter account his attitude toward the question of specific terminology for elements of an "island-formation" permits of much clearer description for the cranial region than for the abdominal region. On page 133 (*ibid.*) he gives a figure of "island-formation" as it takes place in the anterior cardinal vein of *Tropidonotus*. Here, in contrast with his usage for the posterior cardinal (consult my figure 8) he retains the term "anterior cardinal" for that "Schenkel" of the "Insel" which represents the original anterior cardinal line; for the newly established "collateral Venenbahn" he makes use of the specific, non-cardinal embryological term *Vena capitis lateralis*. Toward clarity of description this is a distinct advance. It would be unfortunate if no system of terminology comparable to this were ever permitted for the veins of the thoracic and lumbar regions.



FIGS. 9, 10, AND 11. DIAGRAMS TO ILLUSTRATE THE FORMATION OF THE V. CAVA INFERIOR IN THE RABBIT

(Modified from Hochstetter, 1902, in Hertwig's *Handbuch*, p. 142, figures 166–168.) In the original figures all veins are shown in solid black. Attempt is made here to indicate the derivatives of the original cardinal veins by lighter shading. For explanation of labelling, consult the preceding figures. *Ur.*, ureter. *V.ca.p.*, posterior cardinal vein. *V.sp.i.*, vena spermatica interna. *V.c.i.*, vena cava inferior, postrenal section. In the original of fig. 9 the veins which have more recently been called "subcardinals" were designated by Hochstetter as "Urnierenvenen." In 1893 he had used the latter term to designate the cranial remnants of the "ventral *Schenkeln*" of his "Cardinalveneninseln." In figure 10, the latter usage has been substituted.

For the original vascular path medial to the cranial ganglia the term *v. capitis medialis* had been in frequent use. For it, Sabin (1917) suggested the etymologically impossible substitute *Vasa primitiva*.

From a program of work so epoch-making and extensive as that which Hochstetter carried out, it is difficult, and at all events arbitrary, to select for discussion his greatest individual contribution to the study of veins. In this connection, his figures 14 and 19 of his *Tafel* 22 are of outstanding importance (consult my figures 6 and 7). So far as I am aware, these are the first figures ever published showing coexistent anlagen of mammalian postrenal vena cava along with the original mesonephric sections of the posterior cardinal veins. I can find no evidence, either by way of illustration or discussion, that any predecessor of Hochstetter ever saw the true *forerunner* of postrenal vena cava and mesonephric posterior cardinal as parallel, coexistent structures in any individual mammalian embryo.

SABIN'S INTERPRETATION OF RATHKE AND KERSCHNER

On page 27, Sabin (1915) makes this statement, which I can regard only as being without foundation of fact:

> Rathke, however, in his subsequent work, published in 1838, gave up the theory that the lower segment of the inferior vena cava came from the posterior cardinal vein, because he had specimens in which two vessels were present, namely a vessel medial to the kidney, making the anlage of the vena cava, and a vessel lateral to the kidney or the posterior cardinal vein (see Kerschner, p. 812).

Without success may one search page 812 of Kerschner (1888-a) for any statement lending itself to such an interpretation. The same may be said of the entirety of Kerschner's writings. Not once did Kerschner state that Rathke had seen both the above-mentioned vessels (as we know them at present) coexistent in the same mammalian embryo. The preparation of Kerschner's account preceded the publication of that of Hochstetter (1888-b) in which the latter observer mentioned for the first time his mammalian "Cardinalveneninsel." Again on page 27 (1915) Sabin states:

> In 1888 Kerschner analyzed the views of Rathke and Hochstetter and concluded that the lower segment of the inferior vena cava could not be a transformed posterior cardinal vein for two reasons: first, the vena cava has a position more mesial and more ventral than the posterior cardinal ever has; and secondly, at a certain stage both veins are present in the same specimen. This sums up the whole question . . . . .

I have searched every page ever written by Rathke upon the development of the venous system. I find no evidence that he ever saw "both veins present in the same specimen" of a mammalian embryo. Let us now consider Kerschner's interpretations. In the first place, if (as quoted from Sabin) Kerschner stated that the postrenal part of V. cava has a position more *ventral* than the posterior cardinal ever has, that alone should arouse our suspicion of Kerschner's incompetence to "sum up the whole question" of the development of the V. cava. The weakness of Kerschner's argument did not remain unnoticed by Hochstetter. On pages 871–2 (1888-a) the latter discusses the point:

> K. folgert dann weiter: "Ein medial und ventral von den Urnieren (den Nieren) gelagerte Gefäss kann der Cardinalvene nicht entsprechen." Woher Herr K. die Kentniss über eine so eigentümliche Lage der hinteren Hohlvene hat, ist mir ziemlich rätselhaft geblieben . . .

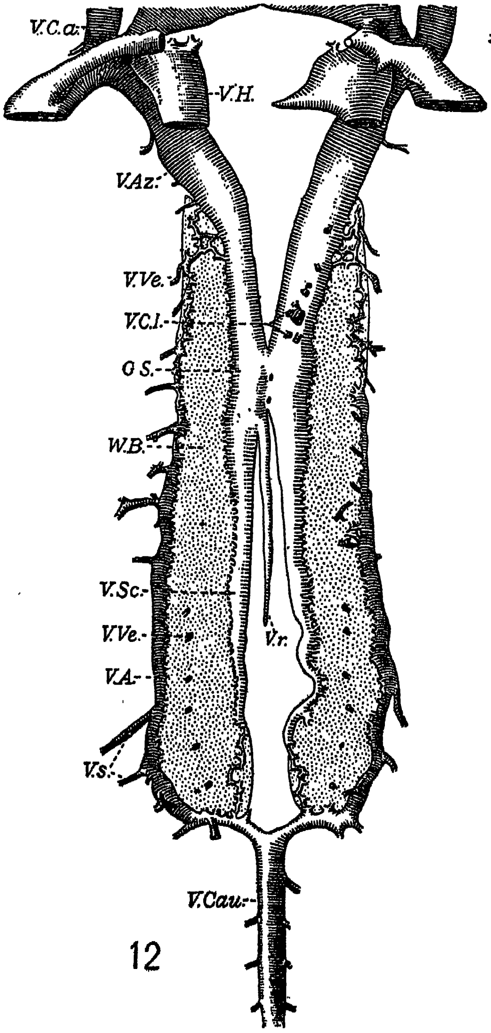
Hochstetter then stated that the anlage of postrenal V. cava is always *dorsal* and medial to the right mesonephros. Evidently his objection to Kerschner's description had to do with the supposed ventral position of the vein with reference to the mesonephros. Sabin (1915, p. 25) quotes exactly the same lines from Kerschner's account (1888-a, p. 813) and pronounces his statement to be "entirely correct." We have, then, a situation requiring to be explained.

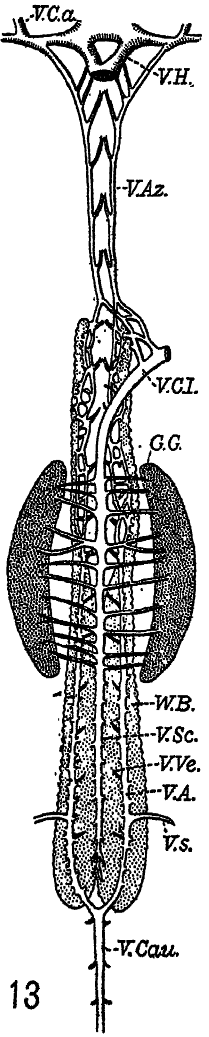
WHAT DID KERSCHNER MEAN?

After much careful study of the writing of Kerschner, I have with some hesitancy come to the conclusion that he supposed the right revehent mesonephric vein (early *right inferior subcardinal* of F. T. Lewis and more recent authors) to be the anlage of normal postrenal V. cava of the ordinary eutherian mammal. If this conclusion be justified, then Kerschner, at least, was probably influenced by Stark.

Kerschner's central purpose (1888-a) was avowedly the interpretation of the more common type of anomalous "doubling" of the postrenal V. cava. He had evidently found an instance of "hohe Teilung" of the vein, in which the left homologue of normal postrenal V. cava had persisted parallel to the normal vessel. In terms of this he attempted to interpret what he could find in the literature upon the developmental process involved. Taking this anomaly as a point of departure, he stated (*loc. cit.*, p. 815) that normal postrenal V. cava is a unilateral product of bilateral anlagen; that two bilaterally homologous longitudinal anlagen are united by two transverse anastomoses; that one of these anastomoses occurs at the renal level, forming the left renal vein; that the other normally occurs at the level of the lower limbs; that if the latter anastomosis fails to form, a "left inferior V. cava" joins the right at the renal level; that these postrenal bifurcations (roots of the V. cava) are comparable to attenuated Vv. iliacae communae. On page 819 (*ibid.*) Kerschner defines the term "iliac vein" as he uses that term for mammals, and as he claims it was used by Rathke and by Nicolai. He says this vein consists developmentally of two parts: a lateral portion formed from the anastomosis between posterior cardinal and the root (*Wurzelast*) of the vena cava (subcardinal-postcardinal anastomosis of recent authors), and a longitudinal part, the root of the vena cava itself. He states that this is not Hochstetter's use of the term iliac. On page 815 Kerschner (1888-a) concludes "dass die Vv. iliacae primitivae der Vogel den beiden Wurzeln einer gedoppelten Cava, also den wirklich 'verlängerten' Vv. iliacae comm. gleich zu setzen sind." He also states on the same page that the terms for the parts of the cava of birds are directly applicable to the cava of mammals, this statement follows those concerning the "doubled" cava of mammals. He states on the same page that the Venae renales revehentes of reptiles and amphibians correspond to the Vv. iliacae of birds. If, therefore, as stated by Kerschner (1888-a, p. 815) the normal "double" V. cava of the seal, or the abnormal double V. cava which he attempted to interpret involved a persistence of the left homologue of normal postrenal V. cava (which he would regard as the left "root of the V. cava"), it follows that he derived normal typical eutherian postrenal V. cava from the mammalian homologue of the right revehent mesonephric vein of the anamnia. The early revehent mesonephric veins of anamnia were termed "subcardinal veins" by F. T. Lewis in 1904 (consult my figures 12 and 13). Von Baer and Rathke frequently called the caudal portions of the revehent mesonephric veins of lower vertebrates "roots of the V. cava." Hochstetter, Kerschner, Balfour, Minot, and many others called the mammalian homologues of the caudal portions of these revehent vessels "roots of the V. cava." Lewis (1902) called these "roots of the V. cava" of mammals "inferior divisions of subcardinal veins" in the youngest stages figured by him.

We have noted the claim of Sabin to the effect that Kerschner correctly interpreted mammalian postrenal vena cava on the basis of these propositions: that postrenal vena cava and posterior cardinal vein coexist in the same specimen, separated from each other by the kidney, in such arrangement that vena cava is on the medial side of the kidney, while posterior cardinal is lateral to it; that Kerschner derived this notion from Rathke and Hochstetter. It is clear that if this were true, Kerschner must have believed in something at least faintly resembling the "Cardinalveneninsel" of Hochstetter. Hochstetter's discovery of his mammalian "Insel" had, however, not been published prior to the time of Kerschner's account.





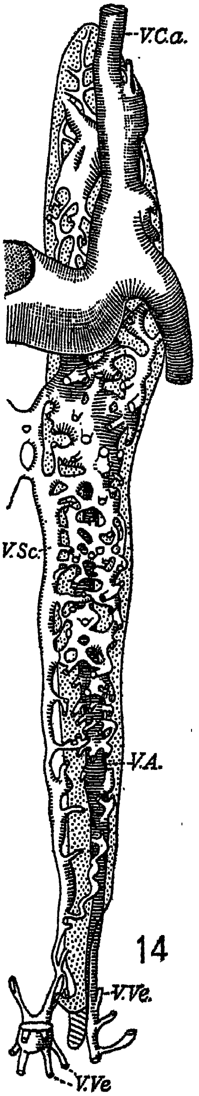


FIG. 12. RECONSTRUCTION OF THE VEINS OF A 51-MM TORPEDO EMBRYO

(After F. T. Lewis, 1904, figure 6, p. 268.) *V.C.I.*, vena cava inferior. *V.Az.*, "mesonephric azygos vein" (renal portal vein; advehent mesonephric vein of Hochstetter; posterior cardinal vein). *V.Sc.*, "subcardinal vein" (revehent mesonephric vein of Hochstetter, 1892, Taf. 17, figure 9). *V.H.*, hepatic vein. *V.r.*, vein from rectal gland. *G.S.*, genital sinus. *W.B.*, Wolffian body.

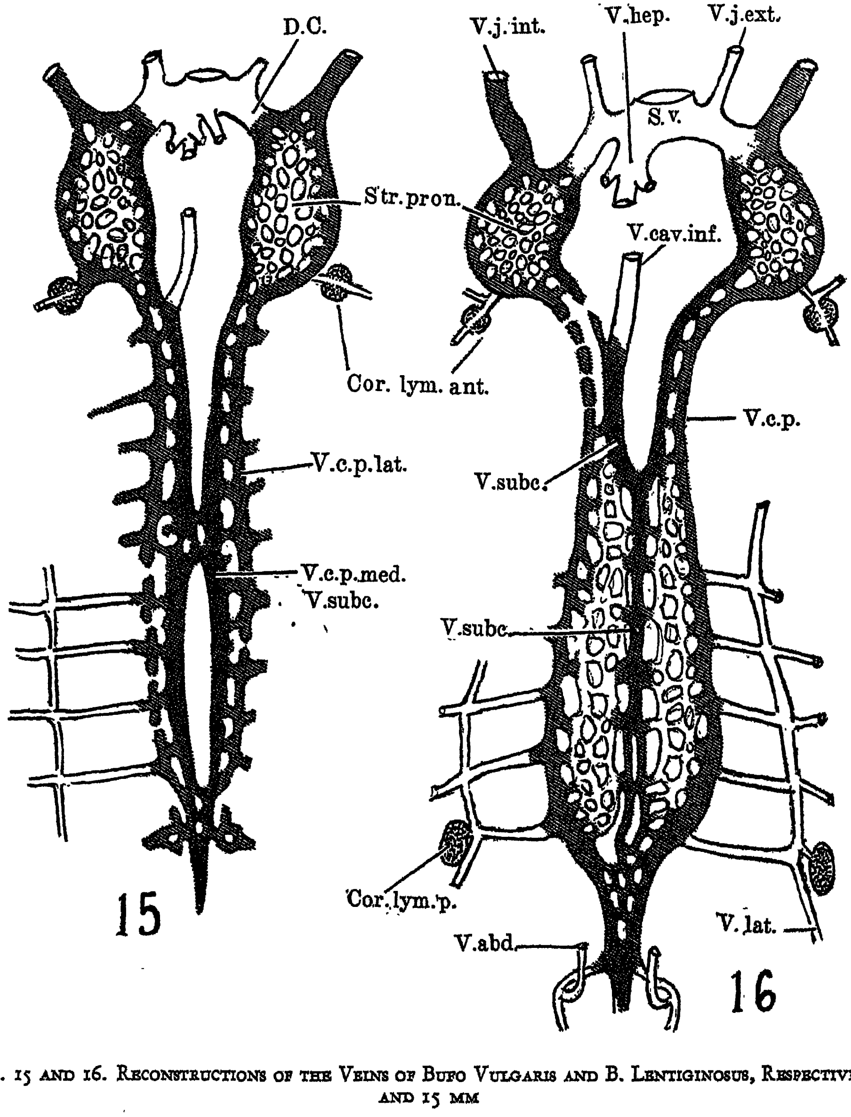
FIG. 13. INJECTION OF THE VEINS IN AN ADULT NECTURUS PREPARED BY THE LATE PROFESSOR PRENTISS

(After F. T. Lewis, 1904, figure 7.) *V.Ve.*, vertebral vein. *G.G.*, genital gland. *V.s.*, somatic vein. (Other abbreviations as in figure 9.)

FIG. 14. RECONSTRUCTION OF THE NETWORK OF SINUSOIDS IN THE LEFT WOLFFIAN BODY OF A 5 MM. LACERTA

(After F. T. Lewis, 1904, figure 8.) Compare with figures 12 and 13, and with Hochstetter, 1892. For explanation of the labelling, consult the two preceding figures.

Turning to pages 821–823 (1888-a) we find that Kerschner did describe a "Cardinalveneninsel" with coexistent medial and lateral "Schenkeln." The "Schenkeln" lie on opposite sides of the kidney.



FIGS. 15 AND 16. RECONSTRUCTIONS OF THE VEINS OF BUFO VULGARIS AND B. LENTIGINOSUS, RESPECTIVELY 7 AND 15 MM

(After Kampmeier, figures 3 and 5, pp. 88 and 89, 1920.) In figure 15, the revehent mesonephric vein (here called medial part of posterior cardinal vein) is well formed (*V.c.p., med.*), while the advehent mesonephric vein (here called lateral portion of the posterior cardinal vein) is only in the process of formation as fusions between adjacent intersegmental tributaries to the more medial vein. Compare with F. T. Lewis (1904), figure 5. In figure 16, the revehent mesonephric veins are called "subcardinal" while the advehent ones (*V.c.p., lat.*) are called posterior cardinal. For abbreviations and fuller explanation consult the original figures.

In connection with the "Insel" the previous writings of Hochstetter (1888-e) and of Rathke are discussed. Unfortunately the animal in which Kerschner's "Insel" is discussed is an amphibian, whose kidney, needless to say, is not a metanephros. It therefore possesses no post-metanephric V. cava such as mammals have. As stated by Kerschner, in description of his schema, the lateral "Schenkel" of this last-discussed (amphibian) "Insel" is the advehent mesonephric (posterior cardinal) vein. The medial "Schenkel" of his amphibian "Insel" is the revehent mesonephric vein (*loc. cit.*, p. 821). Kerschner (alluding to the amphibian "Cardinalveneninsel") states on this same page: "Der rechte mediale Schenkel . . . . stellt die Fortsetzung der Cava dar (die meisten Säuger)." He derives his schema of "Inselbildung" from the figures of Goette (1875) and Hochstetter (1888-e) on amphibians. Kerschner's (1888-a, p. 823) final pronouncement upon Hochstetter is to the effect that the latter (in his mammalian studies) had mistaken the "Wurzeläste der V. Cava" (revehent mesonephric veins, comparable to the "mediale Schenkeln" of amphibian "Cardinalveneninseln") for posterior cardinal veins, and that Hochstetter (1887) had either ignored posterior cardinal veins themselves or failed to see them. In effect, Kerschner claims that Hochstetter had confused the mammalian homologue of medial "Schenkel" of the amphibian "Cardinalveneninsel" with the mammalian homologue of the lateral "Schenkel" of the amphibian "Insel." As a matter of fact Hochstetter (1887-a) had confused the medial "Schenkel" of his later-to-be-discovered mammalian "Cardinalveneninsel" (fig. 5, *V. ca. p.*) with the potential lateral "Schenkel" (fig. 4, *V. ca. p.*) of that "Insel." Kerschner did not know that the amphibian and the mammalian "Inseln" involve totally different medially located structures; invariably he erroneously supposed that mammalian mesonephros and metanephros have identical topographical values for the interpretation of veins. Where he used topographically the term *Urniere*, he (see my p. 187) inserted parenthetically the term *Niere*. Not only did he erroneously state that postrenal V. cava develops medially and ventrally to the mesonephros as well as to the metanephros (a statement quoted and approved by Sabin), but he also stated (1888-a, p. 813) that the mammalian posterior cardinal vein is dorsolateral to the metanephros as well as to the mesonephros. This is likewise far from being "entirely correct." (Compare Sabin, 1915, p. 25.)

OUR DEBT TO HOCHSTETTER AND KERSCHNER

In 1888 both Hochstetter and Kerschner performed genuine service in reviving our interest in the subject of vena cava, and in bringing to light much forgotten history of the study of veins. At the time, each author combined with youthful enthusiasm an inadequate understanding of the subject. At first, Kerschner apparently possessed the wider knowledge of the literature. Hochstetter's knowledge was based upon original observation. He had certainly not availed himself of the existing figures and descriptions of relationships of the posterior cardinal vein. Kerschner wielded his language as a sharp instrument. Hochstetter wielded his language as a blunt instrument. The literature was decidedly enriched.

Kerschner's short articles contain several examples of brilliant reasoning. In one of the best, he states (1888-a, pp. 811–812):

> Auch lassen sich gewichtige Grunde der menschlichen und vergleichenden Anatomie dafür anführen, dass wir Anastomosen-systems längs des Sympathicus je nach der medialen oder lateralen Lagerung zu demselben abermals in zwei verschiedene Ketten zerlegen müssen. Ganz unaufgeklärt ist schliesslich der Wechsel der Lagebeziehung der Cardinal- und Vertebralvenen zur Aorta und zum Sympathicus, der selbst im Beckenabschnitt eine Lageänderung sein dürfte.

At their own loss, subsequent observers have ignored this useful suggestion. (By vertebral veins, the "posterior vertebral veins of Rathke" are implied).

Kerschner pointed out (1888-a, p. 810) the fact (as shown in figures by Haller, 1756) that a portion of the V. azygos reaches to a level decidedly caudal to the renal anastomosis, and thus accompanies a portion of the postrenal V. cava before joining it; that Hochstetter's diagrams (1887-a) failed to explain this fact.

That the human V. azygos anastomoses with V. cava inferior well below the renal level is a familiar fact of ordinary anatomical description. Figures by Poirier and Charpy, Testut, Lazar (Anatomical Plates), and Robinson (1891) show this caudal connection. Yet the later stages of development of this part of V. azygos are explained away by Hochstetter (1902), McClure and Butler (1925), and Butler (1927), either by hiatuses in the figures or by series of dotted lines in that location indicating atrophy of the azygos lines prerenally.

Hochstetter's diagrams (1902, p. 142; see my figure 9) make no provision for the condition pointed out by Kerschner, though his description (1893) of a new part of the V. azygos helps to explain it. Kerschner (1888-a, p. 817) correctly followed certain predecessors when he self-contradictingly stated that for the revehent mesonephric veins of anamnia, the terms *cardinal vein* (equivalent to posterior cardinal of recent authors) and *posterior vena cava* (of earlier authors) served "eben so gut und eben so schlecht."

Although Kerschner (1888-a, p. 820) stated that his views were not in conflict with those of Rathke (1838), Kerschner believed in a "paired anlage" of postrenal V. cava, whereas Rathke (1838) described for it an "unpaired anlage." On page 809 (1888-a) Kerschner noted that many diagrams then in use (see my figure 1) made no provision for the anomalous "doubling" of the postrenal V. cava, though, unlike the diagrams (see fig. 2) by Hochstetter (1887-a), they showed it to be a new formation. Kerschner reviewed the opinion of Krause (1876) that the "superfluous left-sided postrenal V. cava" is a serial continuation and homologue of V. hemiazygos. Kerschner stated his belief that this temporary left lumbar caval vessel was a bilateral homologue of normal postrenal V. cava. On the basis of this, he suggested (p. 809) that normal postrenal V. cava is a serial homologue and continuation of the "vertebral" (non-posterior-cardinal) part of V. azygos. This hitherto unemphasized fact of history is of interest in connection with the theory developed subsequent to Kerschner's account, by Huntington and McClure, Sabin, and Butler.

Removed from context, many statements of Kerschner are quite impressive. For instance, on page 814 (1888-a) he states that so far as their original embryonic plexiform condition permits, V. cardinalis posterior and the anlage of postrenal V. cava inferior are independent structures. The lustre of this remark is dulled by the fact that Kerschner did not even know an anlage of postrenal V. cava when he saw it or, perhaps more correctly, he did *not* know when he was *not* seeing one. F. T. Lewis (1902) makes no mention of Kerschner, but on page 241 Lewis makes this significant statement:

> It has been the custom of certain embryologists to give the name of the whole of the vena cava to one of its parts, namely the subcardinal portion, and even to charge with ignorance those who called other sections of the adult vessel the vena cava.

Undoubtedly the recent tendency has been to accord Kerschner too important a place in the history of the subject, and to misrepresent the views of Hochstetter or to minimize the importance of them.

MISINTERPRETATIONS OF HOCHSTETTER'S VIEWS

On page 236 (1902) F. T. Lewis states that the permanent kidney, coming into contact with the cardinal, may "split" that vessel "to form a loop as figured by Hochstetter." On page 270, Butler (1927) represents Hochstetter as believing that

> the location of the adult vena cava medial to the right kidney and ureter came about by a split in the posterior cardinal vein; this gave rise to a periureteric ring, the lateral half of which was lost, while the medial half persisted to form the main channel.

We have already seen (p. 184) that in one account (1888-b, pp. 939–940), Hochstetter recognized the ventrolateral "Schenkel" of the "Cardinalveneninsel" as the original posterior cardinal vein (*selbst*), and the dorsomedial "Schenkel" as a new "collateral Venenbahn." In his *Bemerkungen zu Zumstein's Arbeit*, Hochstetter (1898, p. 516) makes this statement, which I quote without comment:

> Zumstein beschreibt ferner für denselben Embryo das Auftreten einer Spaltung in der hinteren Kardinalvene, die zur Inselbildung in dieser Vene führen soll. Leider hat Zumstein wieder nicht angegeben wie er sich diese Spaltung in der Kardinalvene zustände kommend denkt und warum er meine Angaben, welche die Bildung der Insel in den hinteren Kardinalvenen einer die segmentalen Venen dieser Gegend in Verbindung setzenden kollateralen Venenbahn entstehen lässt, für unrichtig ansieht. Denn wenn an allen den von ihm untersuchten Embryonen, wie er sagt, der dorsale Schenkel der Insel schon vollständig zu sehen ist, so beweist dies doch durchaus nicht, dass erstens die Insel durch Spaltung der ursprünglich einheitlichen Kardinalvenenbahn entsteht und zweitens, dass ihr dorsaler Schenkel nicht der Ausbildung einer Kollateralen Venenbahn seine Entstehung verdankt.

On page 239 (1902) F. T. Lewis points out an error made by Kollman, who, presumably basing his account on Hochstetter, describes the hepatic part of V. cava as uniting directly with the posterior cardinal vein. Lewis states that "in this he follows Hochstetter's earlier description (1893, p. 569)." Sabin (1915, p. 27) states that Lewis cleared up the existing confusion by showing that the hepatic part of vena cava does not unite directly with the posterior cardinal; that this is the fundamental contribution of Lewis. Again we do well to consult Hochstetter. On page 515 (1898) he states that the hepatic part of vena cava applies itself to the ventral surface of the Wolffian body, a relationship said by Hochstetter (*loc. cit.*) to have been made clear in his account in 1893, but to have been ignored by Zumstein (1898). Hochstetter (1898, p. 515) states:

> Soll die so gelagerte V. cava mit der rechten V. cardinalis, die an der Dorsalseite der Urniere verlauft, in Verbindung treten, so kann dies nur durch ein Venenrohr geschehen, welches von der Cava winkelig abbiegend an der medialen Fläche der Urniere vorbei in die V. cardinalis posterior übergeht. Diese rechtwinkelig auf V. cava und V. cardinalis posterior verlaufende Verbindung ist in meiner Fig. 9 (*Tafel* 21, 1893) aufs deutlichste zu sehen.

On page 569 (1893) his description is not contradictory to the view just quoted. Not only does he describe one large anastomosing vessel (comparable to the subcardinal-posterior cardinal anastomosis of recent authors) at right angles to "vena cava" and posterior cardinal, but he describes several smaller ones said to be reminiscent of the mesonephric drainages from renal portal veins of birds and reptiles (small subcardinal-postcardinal anastomoses of recent authors). Again the inadequacy of his account is largely a matter of terminology. Here he obviously "applied the term for the whole of the vena cava to one of its parts, namely the subcardinal portion," a practice concerning which I have already quoted the comment of Lewis.

Hochstetter's observations have swept wide horizons. Often his most important conclusions are very briefly and casually stated. His work contains great funds of information practically unexplored by recent authors. His short controversial articles are in some ways the most instructive. Much unprofitable future discussion could be avoided in the literature relating to veins, if those of us who are still novices upon the subject were required to read and to cross-index every page of Hochstetter before giving forth our own nascent opinions.

THE WORK OF RATHKE

We may now consider the work of Rathke. In addition to providing information upon points in the work of Rathke which have ordinarily been neglected, I shall attempt to afford answers to these questions which are at once raised if we wish to harmonize the contents of previous reviews with the present review:

(1) Was Rathke (1830-a) so ill-informed as to suppose that the mammalian postrenal vena cava develops lateral to the permanent kidney? (2) Was he unaware that a part of V. cava inferior traverses the liver, and if not, did he believe that a part of the posterior cardinal vein becomes incorporated into the liver? (3) Was the work of Stark the first to set forth correctly the relation of V. cava to kidney and liver? (4) Is there any real evidence that Rathke was influenced by Stark? (5) Was the view of Hochstetter (1887-a) identical with that of Rathke (1830)? (6) Is Rathke's final interpretation reconcilable with that of Kerschner?

I find negative answers to all these questions. Hochstetter answers the fifth negatively. In all other cases where the points are discussed at all, these questions are answered affirmatively in the reviews of Hochstetter, Kerschner, Sabin, and Butler.

Whereas in 1830 Rathke did apply the term "hintere Hohlvenen" to the vessels which we now call posterior cardinal veins, and emphasized the fact of their position dorsal and lateral to the mesonephroi, he certainly was aware that postrenal vena cava (see my figures 26 and 27) lies medial to the kidney. On page 69 (*ibid.*) he stated that his account was only a preliminary one, and that a more complete one was to follow it. In 1830 he barely indicated the main points as he understood them:

that the mesonephric segment of the right "hintere Hohlvene" (posterior cardinal of later authors) undergoes a migration (*Wanderung*) from the dorsolateral side of the mesonephros to the dorsomedial border of that structure and to a position close to the dorsal aorta; that this migration takes place earlier in the cranial part of the mesenophros than in the caudal part; that the mesonephros becomes displaced laterally with the growth of the kidney; that, as a result of the medial migration of the right "hintere Hohlvene," that vessel comes to lie close to the left mesonephros; that as a consequence a venous anastomosis between the two mesonephroi is more readily possible (*loc. cit.*, p. 68) "als wenn jener Venenbahn um seinem ursprünglichen Ort verharrt wäre." He states (p. 69, *ibid.*) that along with this venous cross anastomosis there appear as branches of the transverse anastomosis, two longitudinal vessels on the ventromedial surface of the left mesonephros, the cranial one being in direct line with the caudal one; that "zwei ähnliche Aeste ubrigens verbinden auch die rechte falsche Niere mit der bleibenden hinteren Hohlvene." (These may represent the revehent mesonephric veins and the hepatic anastomosis). Regardless of the fact that in one part of his account he stated that the vessel which we now call right posterior cardinal is the "nachherige hintere Hohlvene," he was probably referring to that part of "bleibenden Hohlvene" located in (what we now call) caval mesentery, rather than to posterior cardinal vein when he stated that the veins upon the ventral surface of the right mesonephros "verbinden sich auch die rechte falsche Niere mit der bleibenden Hohlvene." A vessel on the ventral surface of the mesonephros is obviously not in position to unite that structure with a vessel in the position to which Rathke had described the (vessel which we now call) posterior cardinal as having migrated. It is also very significant that Rathke did not state that the caudal part of the vessel ventral to the right mesonephros formed postrenal V. cava. He states that the portion of the left "hintere Hohlvene" lying in the abdominal region degenerates. The later work announced as a completion of this tentative sketch appeared in 1832. I can find nothing in Rathke's account in 1830 which would lead one to assume either that he was ignorant of the existence of the hepatic part of V. cava, or that he supposed the vessel which we now call posterior cardinal vein could ever become incorporated into the liver. He showed the latter vessel (see figure 24) well removed from the liver.

However disappointing the present-day reader may find Rathke's (1830-a) account just discussed, he is likely to experience genuine surprise at the accuracy of Rathke's (1832) badly neglected accounts of the dorsal body wall veins, especially in the lower vertebrates; here there is almost complete lack of confusion, owing largely to Rathke's employment of the relatively reliable and safe terms *advehent* and *revehent veins* of the embryonic excretory system.

Rathke (1832 and 1839) frequently refers to "the advehent and the revehent veins of Jacobson." In the writings of Jacobson (1815 and 1817) to which I have had access, the terms "advehent and revehent" veins of the embryonic excretory system do not appear. The renal portal veins (advehent mesonephric veins of Rathke) are referred to by Jacobson (1817, p. 148) as the *Vv. renales inferiores;* the revehent mesonephric veins of Rathke (early subcardinals of F. T. Lewis) are called *Vv. abdominales anteriores*, by Jacobson. The latter has often been given credit for the discovery of the revehent mesonephric veins. Also the advehent mesonephric veins (amphibian posterior cardinals) are often called "veins of Jacobson."

In Rathke's account of these veins in reptiles (1832-a, p. 32) there is a perfectly accurate and full description of the advehent and revehent veins of the mesonephros, the great anastomosis between the revehent veins, and the union of the right one with that part of vena cava which traverses the liver. On this same page there is a description of the conditions in an embryo adder so young (according to Rathke's description) that no connection had yet been formed between the right revehent mesonephric vein (early right *subcardinal* of Lewis) and the hepatic circulation, although advehent and revehent mesonephric veins were said to be well developed. This is Rathke at his best.

On page 40 (1832-a) Rathke describes the dextral revehent mesonephric vein of the lizard embryo, and states that it

> hatganz dieselbe Lage wie bei Schlangen, nimmt aus der untern (i.e., ventral) Seite der falschen Nieren eine grosse Menge von Venenzweigen auf, und senkt sich mit ihrem Stamme in einiger *Entfernungen der Gekrösvene* auf, und rechts von dieser in die Leber, wo sie dann als hinten Hohlvene erscheint.

His description of the revehent mesonephric veins of the snake embryo (1832-a, p. 32) contains this statement: "Beide Venae renales revehentes verbinden sich endlich dicht vor der falschen Niere der rechten Seite einem sehr spitzen Winkel zur Vena cava."

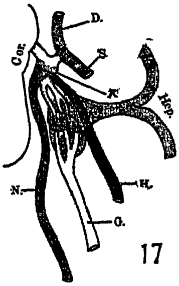
Rathke's description of the Vena renalis advehens of the Boa Constrictor embryo (1832-a, p. 32) is clearly reminiscent of his earlier (1830-a) description of the mesonephric segment of his mammalian "hintere Hohlvene" (posterior cardinal vein of present terminology). He stated that in the snake embryo the advehent mesonephric vein "lauft nach vorne und oben hinauf, legt sich an die äussere Seite der falschen Niere, und zwar ganz nahe am obern Rande derselben . . . ." Of his "hintere Hohlvene" in the mammalian embryo he had stated (1830-a, p. 64): "Auf einem jeden dieser genannten Organe (der falschen Nieren) und zwar auf der äusseren Seite ganz in der Nähe der oberen Rande derselben dicht über dem Eier und Samenleiter, verlief von hinten nach vorn eine Vene . . . ." The latter vessel is shown in Rathke's Tafel 1, Figure 1 (1830). This figure is reproduced as his *Tab.* 4, figure 1, (1832-b) and it is copied as figure 24 of the present account. It seems unreasonable and unjust to infer that Rathke was unaware that a part of the V. cava traverses the liver, or that the work of Stark supplied him with his first information to that effect. When he described his "hintere Hohlvene" as migrating from the dorso-lateral border of the mesonephros "gegen die Aorta hin," he can scarcely be accused of supposing that an intra-hepatic vessel could ever lie against the aorta. He used the too-inclusive term "hintere Hohlvene" at times to designate part of the vessel, such as the postrenal part or that part in the caval mesentery. This is insufficient reason for supposing that he knew nothing of the hepatic part of V. cava or its development. More recent writers who have criticized him on this point have actually called revehent mesonephric veins "V. cava inferior." Again, in 1832, so far as the mammal is concerned, Rathke made no effort to describe the development of the hepatic part of V. cava. He had some knowledge of the development and function of the structure which, after Hochstetter, we call "caval mesentery." This he described developmentally (1832-b, p. 49) as "eine beträchtliche Ablagerung von dichtem Schleimstoffe," which (he states) serves as a passage for the V. cava. He is of the opinion that in 1806 Oken first correctly interpreted it in the dog embryo (Oken und Keiser's Beiträge zur vergl. Anat., Heft 2) and called it "die markige Brücke." Rathke calls it "die Okenschen Brücke." Hochstetter (1893, p. 564) awards credit for the original discovery of the structure to Goette (1875) in preference to Goette's successors: Lockwood, His, Ravn. I offer this detail as further evidence that Rathke knew that V. cava traverses the liver. The existence of the hepatic part of human V. cava inferior had been commonplace knowledge for several centuries. Cuvier, J. F. Meckel (1831, *Th.* 5), and numerous predecessors as well as contemporaries of Rathke were aware of it in mammals other than man. Meckel (1831) classified vertebrates upon the manner in which the venous blood from the caudal part of the dorsal body wall reaches the heart. He placed the dipnoi, amphibia, and what we now call amniota in a group in which this drainage traverses the liver. Von Baer gave evidence of his mastery of the subject of hepatic vena cava from its developmental side, before Stark expressed himself upon that subject. Rathke (1833) gave a very complete discourse upon the relation of omphalomesenteric veins to yolk sac and liver. For a somewhat different estimate of Rathke and Stark, consult the accounts of Kerschner (1888-a, p. 812), Hochstetter (1893, p. 611), and Butler (1927, p. 269). I shall quote only Hochstetter, who states:

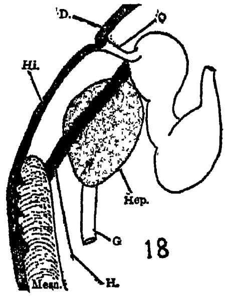
> Stark ist der Erste, welcher angiebt, dass das Endstück der V. omphalo-mesenterica später zum Endstück der V. cava inferior werde und das die Strecke der Hohlvene zwischen Leber und Nieren mit dem Auftreten dieser Organe zur Entwicklung komme.

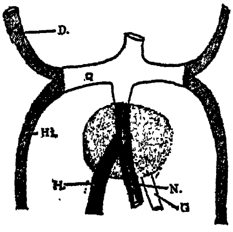
Rathke's account of the V. cava in mammals in 1832 (b), incidental to an account of the genital system, is essentially a reiteration of his statements in 1830, with certain details added. Here (*loc. cit.*, p. 82) he definitely describes his "hintere Hohlvene" as "dissociating itself" from the right "falsche Niere" and taking up a position lateral to and close to the aorta. He states that his description applies almost entirely to the pig. He describes the disappearance of almost all the transverse veins on the dorsal side of the mesonephros, and their functional replacement by one large transverse stem. He gives a clear description of the veins upon the medial surface of the mesonephros and gives their history probably more adequately than any subsequent author has done. He gives a clear description of the origin of the renal drainage into the cross-anastomosis between the medial veins of the mesonephros. He describes vessels for the earlier and the later drainage (consult my figures 26 and 27) of the gonad of the ungulates. He states that with the descent of mesonephros and gonad, the original caudal mesonephric tributaries to the ungulate postrenal vena cava enlarge to produce sex veins entering the latter vessel just cranial to the Vv. iliacae. This he would seem to have regarded as a peculiarity of the ungulate embryo. (Consult Butler (1927) and Reagan and Tribe (1928-b, p. 492).)

THE WORK OF VON BAER

We may now consider the work of von Baer, then the work of Stark, after which we may return to the final view of Rathke. In 1828 (*Entw. der Thiere, Th.* I, p. 71) von Baer described clearly, under a terminology of his own, those vessels which we now call Vv. cardinales anterior and posterior, and ductus Cuvieri. His description applies to the five-day chick embryo (figures 17, 18 and 19). He described on each side a "Drosselvene" which drains caudally to meet a posteriorly located, cranially coursing vessel. This vessel is described thus: "Im untern Rand jeder Bauchplatte ist eine Vene, die mit der Drosselvene jeder Seit vor dem Eintritt in das Herz sich verbindet." This hinder vein is designated as an "Intercostalvene." In a footnote on page 136 of the second part of his *Entwickelungsgeschichte* he stated that his preceding term was the result of a typographical error; that he had meant the vessel to be called "Subcostalvene." On page 71 (1828), in addition to vessels clearly recognizable as Vv. cardinales posteriores of present terminology, he described on each side ventro-medial "Gefässstämme, auf denen die Wolffschen Körper sich







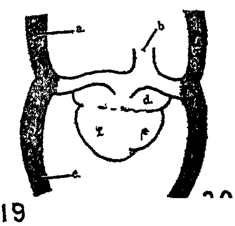


FIG. 17. ENLARGED DETAIL FROM A DIAGRAMMATIC SAGITTAL SECTION OF A FIVE-DAY CHICK EMBRYO

(Simplified from von Baer's *Tafel* 2, figure 8, 1828.) *G*, "Gekrösvene" entering the liver (Hep.); *H*, that part of V. cava within (what is now termed) the caval mesentery; *Hi*, "hintere Hohlvene"; *K*, "Körpervenenstamm"; *Vv.h.*, hepatic veins; *N*, "Nabelvene"; *Cor.*, heart; *D*, "Drosselvene" (equivalent of V. cardinalis anterior); *S*, "Subcostalvene" (equivalent of V. cardinalis posterior). In the original figure, no attempt was made to show through the liver as a transparent object that part of V. cava passing within the right lobe of it. The "Gekrösvene" was shown in orange color. The other veins were shown in blue.

FIG. 18. ENLARGED DETAIL FROM VON BAER'S TAFEL 4, FIGURE 17 (1837)

The portion of von Baer's manuscript describing several of his illustrations was published only posthumously and edited by L. Stieda, who states that the manuscript contains no detailed explanation of the figure. According to von Baer's general description, the structures may be believed to be as follows: *D*, "vordere Wirbelvene" (equivalent of V. cardinalis anterior); *H*, "Hohlvene"; *Hi*, "hintere Wirbelvene"; *G*, "Dottersacvene"; *Hep.*, liver; *Q*, "der venose Querstamm." The figure probably represents a five-day chick in left-lateral view.

FIG. 19. ENLARGED DETAIL FROM VON BAER'S TAFEL 4, FIGURE 10 (1837), SHOWING IN VENTRAL VIEW THE VEINS NEAR THE HEART OF AN AVIAN EMBRYO

(Abbreviations as in the previous figure; in both copies the legends are changed for the sake of uniformity.) *N*, "Nabelvene."

FIG. 20. DORSAL VIEW OF THE HEART AND RELATED VEINS OF A "YOUNG" SHEEP EMBRYO

(After Rathke, 1830-a, *Tafel* 1, figure 1.) *a*, "vordere Hohlvene"; *b*, "Lebervene (nach vorn umgeschlagen)"; *c*, "hintere Hohlvene"; *d*, atrium; *e* and *f*, indications of the ventricles.

bilden . . . . und also die Hauptwurzeln der untern Hohlvenen wären." These "roots of the vena cava" (revehent mesonephric veins) are the caudal parts of early "subcardinals" of recent authors. It is interesting to note that authors of the time thought the mesonephros of amniotes to be a product of the vascular system. On page 98 (1828) he suggested that further study might demonstrate an excretory function of the amniote Wolffian body comparable to that of the kidney of fishes. He attempted (p. 97) to determine the nature of the Wolffian body and vessels by means of injecting the revehent veins, but found all the mesonephric structures obscured by the injection.

Space does not permit a reiteration of all the statements of von Baer which prove that he had a knowledge of the hepatic part of the V. cava. My figures 17, 18, and 19 contain parts of von Baer's Tab. 3, figure 2 (1828). On p. 59 (*ibid.*) he describes accurately the formation of the liver in relation to the omphalomesenteric veins. On page 93 he describes the course of the "Nabelvene" in the liver and states that it

> verbindet sich . . . . dann am vordern Ende dieses Organs mit einer Lebervene, die sich sogleich in die Hohlvene, deren Stamm von oben sich in die Leber eindrückt, einmündet. Mann kann also fast mit demselben Recht sagen, dass die Nabelvene in den Stamm der Hohlvene geht, oder dass sie *in* eine Lebervene sich mündet. Der Theil der Nabelvene, welcher nach der Vertheilung in die Leber bis zum Hohlvenensystem reicht, wäre dem ductus venosus Arantii der Säugethiere zu vergleichen.

The relation of his "stem" of the V. cava to the Wolffian body is discussed on his page 81 (1828, *Th.* 1): "Am 5ten Tage sieht man deutlich den Stamm der Hohlvene mit vielen kleinen Wurzeln aus der innern Seite der vordern Enden beiden Wolffischen Körper hervortreten und hinter der Leber hinaufsteigen." Again on page 98, concerning the chick,

> dass vom fünften Tage an deutlich aus dem vordern Ende des Wolffischen Körpers eine starke Vene hervortritt, die mit, oder vielmehr jetzt den Stamm der hintern Hohlvene eben so ausmacht, wie in später Zeit die beiden Hauptwurzeln der hintern Hohlvene . . . hervortreten.

From a posthumous supplement to *Theil II* of von Baer's *Entwickelungsgeschichte* (the supplement was edited by L. Stieda, in 1888) we find that the Manuscript for *Theil II* was finished in 1834. On page 136 of this account (Theil 2) the following occurs:

> Diese hintere Hohlvene ist noch . . . . sehr kurz. Man sieht dann aus der innern Fläche des vordern Endes jeder Primordial-Niere einen Blutstrom hervortreten. Beiden laufen zusammen in ein Stämmchen, das, wie der Erfolg lehrt, die hintere Hohlvene wird. . . . . sie geht an der obern Wand der Leber vorbei und wird hier ein Zweig des allgemeinen Venenstämmes.

Unfortunately it is impossible to discuss fully the beautiful work of von Baer (1834) upon the porpoise. He describes a "double" postrenal V. cava, the absence of azygos veins, and especially the primitive, plexiform (*geflechtartig*) condition of the venous system. For the information of those who prefer to believe that our fundamental concepts of the vascular system have been arrived at only recently by a fortunate few, this passage from von Baer's (1834) page 10 (402) is offered:

> "Überhaupt scheint mir auch darin die Familie der Cetaceen den niedern Wirbelthieren sich zu nähern, dass das Venensystem viel weniger dem Arteriensystem gleich bildet ist, als in den übrigen Säugethieren.
>
> Die frühzeitige Auflösung der Venenstämme in Geflechte, oder richtiger gesprochen, indem wir von der Peripherie nach dem Centrum vorschreiten, das späte Sammeln der Venengeflechte in Stämme, wodurch die Cetaceen sich vor andern Thieren auszeichen, scheint für die Vergleichende Anatomie von grosser Wichtigkeit. Bedenkt man nämlich, dass in Embryonen Zustande auch die grossern Gefäss-Stämme, und namentlich die Venen, geflechtartig auftreten, dass, um nur *ein* bekanntes Beispiel

> hervorzuheben, in Fisch-Embryonen selbst die Aorta durch ein weites Geflecht in den Stamm der hintern Hohlvene übergeht, wie Döllinger so schön dargestellt hat, so zeigen die Cetaceen hērein nicht nur eine gewisse allgemeine Embryonen-Aehnlichkeit, sondern man kann auch, wenn man weiter sieht, erkennen, wodurch diese allgemeine Embryonen-Aehnlichkeit selbst hervorgebracht wird."

Von Baer then states that John Hunter (1787) saw and noted conditions of this sort in the whale. On page 332 of Hunter's account there is reference to the sluggish manner of circulation in the whale, and to the tendency of the vascular system here to maintain a widespread net-like condition, which Hunter described as reminding him of the pampiniform plexus of the bull. Consulting Allen Thomson (1832), we find that Hunter correlated the retention of embryonic plexuses in the adult sloth with the sluggishness of habits and of circulation in these creatures. Spallanzani (1801) noted that in regenerating tails of urodeles the first vessels are capillary plexuses similar to those of early embryonic development; that the great caudal vessels are regenerated out of such plexuses.

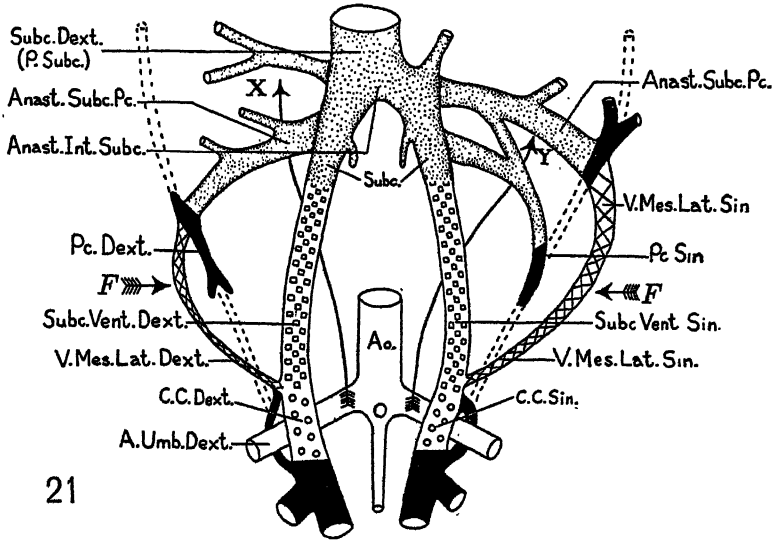


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FIG. 21. RECONSTRUCTION OF A PORTION OF THE VENOUS SYSTEM OF A 14-MM. SHEEP EMBRYO

(Harvard Embryological Collection, Series 1106, after Butler, 1927, figure 9, p. 299.) *P.C., dext. et sin.*, degenerate remains of Vv. cardinales posteriores; *Subc.*, "subcardinal veins"; *Subc. Vent.*, "Ventral subcardinal veins." The figure is of interest in making intelligible the descriptions given by Stark (1835), and in rendering improbable the supposition that Rathke ever saw "cardinal veins" (posterior cardinals) and the anlage of postrenal V. cava present in any given specimen of sheep embryo. Postrenal V. cava has not yet appeared.

In 1835, von Baer published his beautiful and accurate work upon the development of the teleost fish. Here he abandons the terms "Drosselvene" and "Subcostalvene." For them he substitutes the terms "vordere Vertebralvene" and "hintere Vertebralvene." The common stem which unites the two veins is called "truncus transversus" (consult my figure 23). It should be noted at once that these vessels are comparable to our present badly named anterior cardinal, posterior cardinal, and the duct of Cuvier in fishes. They are not to be confused with the "vertebral veins" of Rathke (1838).

In 1835, von Baer objected to the use of the term "hintere Hohlvene" as Rathke had employed it. On page 25 (*ibid.*) he states:

> Diese *hintere Vertebralvenen* sind allerdings wohl dasselbe, was man in Fischen gewöhnlich die Hohlvene (denn man spricht gewöhnlich nur von Einen) zu nennen pflegt, aber wohl mit Unrecht, wenn man damit dasselbe Blutgefäss zu bezeichen glaubt, das in Säugethiere diesen Namen führt.

Then in a footnote he states that for the teleost fish the hepatic (omphalo-mesenteric) circulation contains the only venous structure to which the term V. cava is applicable. Von Baer's term "posterior Vertebral vein" fared no better in the evolution of our terminology than did his term "Subcostal vein." Yet these terms represent a reaction against the misnomer "V. cava inferior" as it had been employed to designate the earliest veins in the embryonic bodies of amniotes and the adult posterior veins of lower fishes. His terms represent progress in the direction of liberating embryological terminology from the domination of adult anatomical terminology. His work was dedicated to Rathke.

THE WORK OF STARK

The primary purpose of the work of Stark (1835) was to portray and to explain a number of anomalies of the veins. Among his mammalian anomalies were five instances in which the postrenal V. cava drained by a path, not through the liver but through the enlarged azygos veins. The latter, in addition to their normal function, had assumed that of draining the entire infrathoracic region, in the absence of the part of V. cava normally found in the caval mesentery. In adult amphibians, reptiles, birds, and mammals, Stark attacked the problem experimentally by ligating the V. cava at the level of the caval mesentery and injecting the veins at points caudal to the ligature. He studied the collateral venous lines by which the injecting-mass reached the cranial regions. He also injected mammalian embryos and foetuses. His chief interest was that of thoracic drainage. To the embryonic mammalian structures to which Rathke had (1830) so unfortunately applied the term "hintere Hohlvenen" Stark applied the equally unfortunate adult terms V. Rathke (1830-a), according to Stark, made two statements which Stark regarded as incorrect. The former said that the sheep has no (dextral) azygos veins; he said (according to Stark) that the hepatic vein enters the structure which we now call the right duct of Cuvier. I am unable to see that this implies that Rathke believed the cranial segment of (what we now call) posterior cardinal vein becomes incorporated into the liver. Stark (1835, p. 27) offers the criticism of Rathke, of which the following is an attempted translation:

> One of these veins (*hintere Hohlvenen*), the sinistral one, our eminent Authority maintained to be the V. hemiazygos, while the other one was the V. cava inferior. With the first part of his assertion I am entirely in agreement. It can not be reasonably doubted that the left one is the V. hemiazygos. But I can not concur with him that the dextral one is the V. cava inferior. I should for my part take it to be the V. azygos. He seeks to champion this opinion by observing that the V. hepatica is admitted to the trunk which is formed by this vein with the jugular vein, and that in the sheep the dextral *V. sine pari* is obviously lacking. Begging the pardon of a man for whom I have the profoundest respect, this statement is incorrect . . . . the other argument which he derives from the inosculation of the V. hepatica into the common trunk of the right hand side does not, I think, count for much, since the V. hepatica almost invariably enters the cavity of the atrium some distance from the V. cava superior, and, indeed, from the lower side. . . . .

Now the existence of a normal right azygos vein in human anatomy had been recognized since Vesalius (1543) published his *Fabrica*. The existence of a hepatic part of V. cava inferior was known even earlier. Whether Rathke (one of the greatest anatomists of his time), like a large number of contemporary comparative anatomists, (consult Meckel, 1831, *Th.* 5) positively knew that many mammals and man have functional dextral azygos veins, I should be reluctant to offer doubt. Granted that he was to this

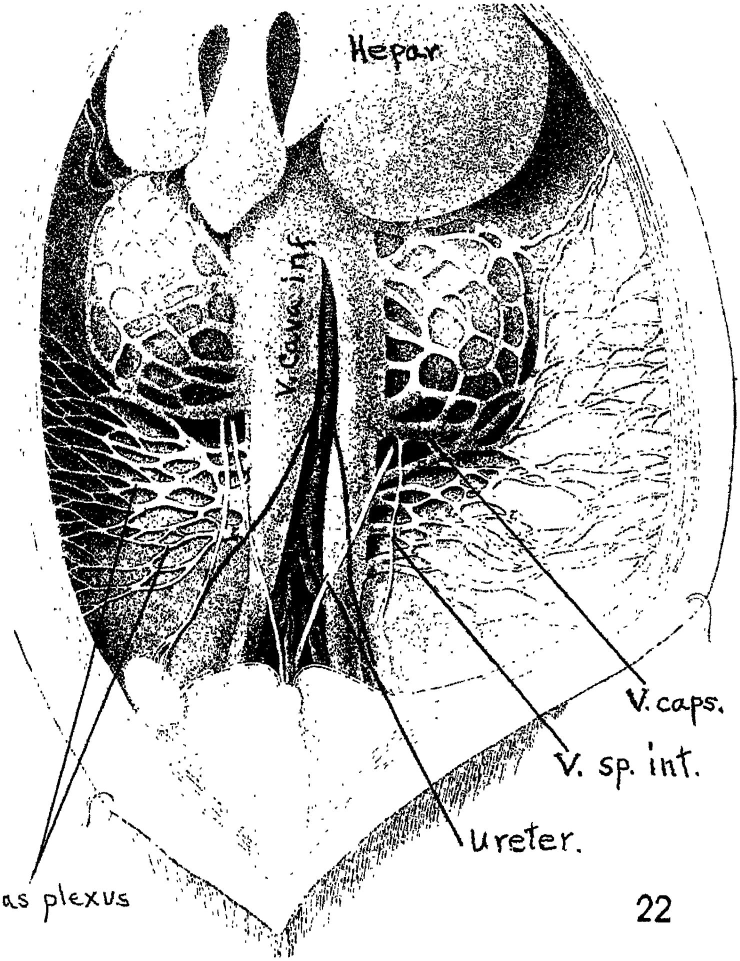
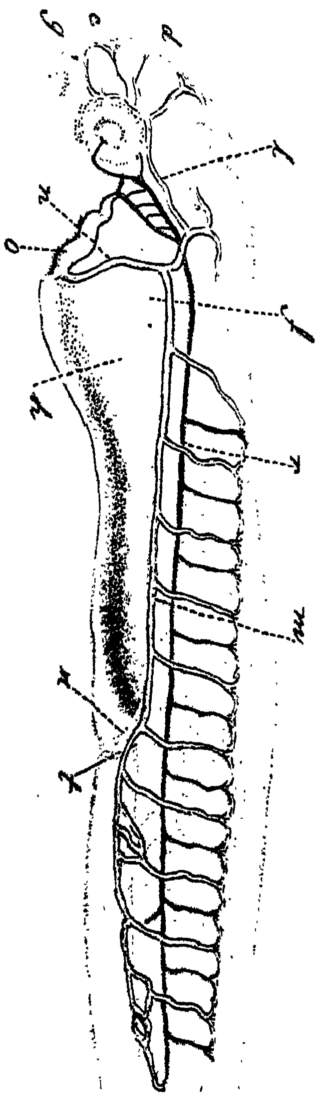


Fig. 22. Veins of Dorsal Wall of Abdominal Region of a Seal

(From A. Burow, 1838, *Taf.* 7.) The figure shows a normally persistent left homologue of postrenal V. cava in addition to that structure; these are both called iliac veins in the original figure. The internal spermatic veins (*V. sp. int.*) drain into the drainage system of the renal capsule (*V. caps.*). The venous plexuses caudal to the kidneys were called "psoas plexuses." No attempt has been made to carry out the original labelling of the figure. It is hoped that the figure may be of interest in connection with work which greatly needs to be done on the nature and development of the vascularization of the renal capsule. Subperitoneal plexuses continuous with embryonic "psoas plexuses" are reflected around ventrad of the peritoneal cavity. From this general plexiform system are derived the veins of the renal capsule, the ureter, and certain veins of the ventral body wall.

suppose he believed such animals to be devoid of Vv. cavae inferiores; and it is equally absurd to suppose that he believed his right "hintere Hohlvene" to form both vessels in animals possessing both.

Stark (1835, *Tab.* 2. figure 8) gave an excellent figure of a young sheep embryo which had been injected and dissected by Prof. Huschke. The figure itself (consult my figure 25) was drawn by Prof.



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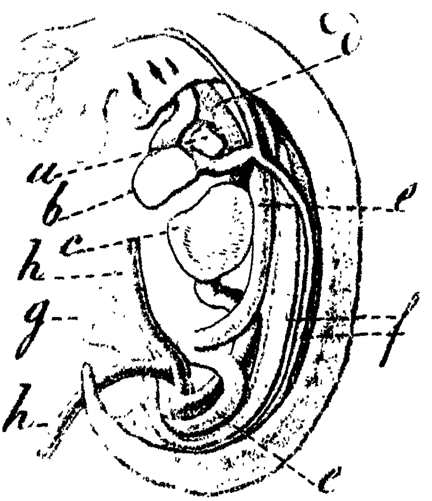

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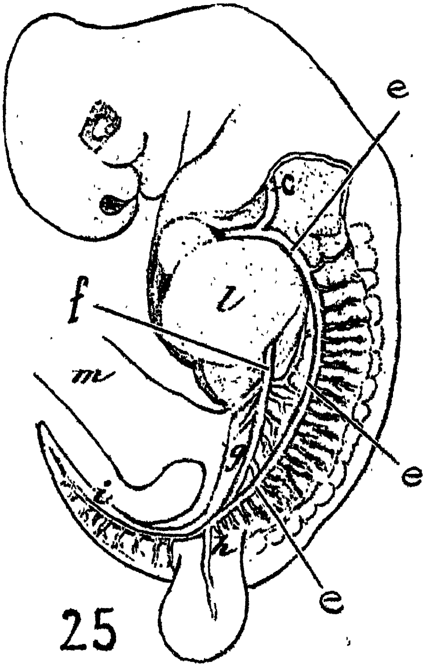

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FIG. 23. THE VASCULAR SYSTEM OF AN EMBRYONIC TELEOST FISH CYPRINUS

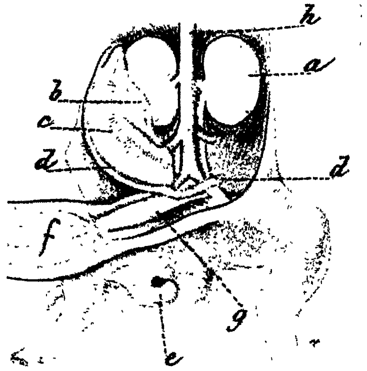
(From photographic enlargement of von Baer's figure 20, 1835.) *f*, anterior extremity; *g*, nasal pit; *h*, yolk sac; *l*, "vordere Vertebralvene"; *m*, "hintere Vertebralvene"; *n*, "Querstamm (truncus transversus)"; *o*, atrium; *r*, aorta dorsalis; *t*, "harnleiter." Note especially the beautifully illustrated intersegmental vessels.

FIG. 24. LATERAL VIEW OF A "VERY YOUNG" SHEEP EMBRYO

(After Rathke, 1830-a, *Tafel* 1, figure 1.) *a*, left atrium; *b*, ventricle; *c*, liver; *d*, "Luftröhre;" *e*, alimentary tract; *f*, "mesonephros and its efferent duct and the *hintere Hohlvene*"; *g*, "funnel of the allantois"; *hh*, the "two Nabelvenen."

Huschke. The embryo is described as having no nose, no eyelids, an incompleted iris, and palp-like limbs. The posterior cardinal (labelled *V. azyga sinistra*) vein which can be seen exhibits no tendency towards degeneration. In the embryos of ordinary eutherian mammals (rodents included) having a non-marsupial type of postrenal V. cava, the anlage of the latter vessel is usually not present so long as the posterior cardinal vessel is so strongly functional as the "V. azyga sinistra" of this figure is shown to be. A vessel (*f*) draining into the liver is called V. cava inferior. This, in turn, drains a vessel (*g*) described as anastomosing caudally and laterally with the "V. azyga sinistra" (*e*) and with the "V. cruralis" (*h*). Throughout its course, the vessel labelled *g* receives mesonephric tributaries described as "V. fine pari contrahens." Stark (p. 29) mentions that "again, in another sheep embryo a little older, Prof. Huschke, who made an injection of the V. cava inferior and thereby filled the V. azygos, distinctly saw the V. cruralis uniting with it." Stark emphasized the fact that in these two sheep embryos only was it possible to obtain conditions such as those shown in his figure just described. His study also comprised relatively older embryos of the sheep, the cow, and man. In the latter he experienced difficulties with injection. He mentioned even larger vessels than his his vessel *g* on the ventromedial surfaces of Wolffian bodies in later stages, but found it impossible to inject the "crural" veins from them; with increasing age, such vessels were found to become even shorter. Concerning his vessel *g* and the general conditions in his *Tab.* 2, figure 8 (see my figure 25) he states (p. 29):

> As, however, we have been able to observe this arrangement of the veins in only one or two cases, I should like to have it confirmed by further experiments on the part of other observers (Cum vero semel iterumque tantum hanc vasorum rationem deprehendere nobis licuit, ab aliis quoque observatoribus eam pluribus experimentis confirmatam velim).



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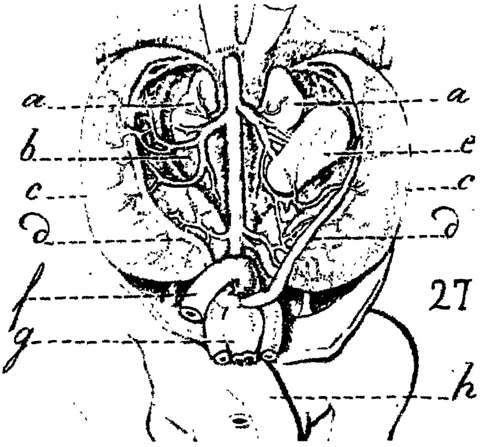

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FIG. 26. DISSECTION OF THE HINDER PART OF A SHEEP EMBRYO WITH BODY WALL, ALIMENTARY VISCERA, AND THE LEFT MESONEPHROS AND GONAD REMOVED

(After Rathke, 1832-b, *Tafel* 3, figure 9.) *a*, metanephros; *b*, gonad; *c*, "Eierleiter oder Samenleiter"; *e*, external genitalia; *f*, umbilical cord; *g*, urinary bladder; *h*, "hintere Hohlvene."

FIG. 27. DISSECTION OF THE HINDER PART OF A PIG FOETUS

(After Rathke, 1832-b, *Tafel* 4, figure 3.) Most of the viscera and the right gonad were removed. *a*, suprarenal gland; *b*, metanephros; *c*, mesonephros; *d*, "Eier- oder Samenleiter"; *f*, hind gut; *g*, urinary bladder; *h*, external genitalia. Note especially the veins taking care of the caudal drainage of the mesonephros.

From Kerschner (1888-a) one gets the impression that Stark actually saw in the figure described the true anlage of postrenal V. cava. The fact that Stark failed to find his vessel *g* in older stages of embryos of different species has been noted. On page 35, in Stark's final summary is this statement:

> As to the part of the V. cava which remains to be perfected between the kidneys and the iliac veins, I was not privileged to see how its nature is changed during development. Until the eyes of man have been able to discern this process, conjecture must be accepted (Quae denique Venae cavae inferioris perficienda restat pars inter renes et vasa iliaca sita, quomodo in ea fabricanda natura versetur, deprehendere nondum concessum fuit. Quod naturae opus priusquam fortuna cuipiam mortalium oculis conspiciendum obtulerit, conjecturae concedendus erit locus).

From what has been quoted, it would seem that Stark did not regard his vessel *g* as the anlage of postrenal V. cava. It is probable that he was dealing with a condition peculiar to the sheep, such as that found by Butler (1927) temporarily to exist in the sheep embryo (consult my figure 21, reproduced from Butler's figure 9). In this figure of Butler's, the posterior cardinal vessels have degenerated far more than they have in the figure from Stark, yet in the figure from Butler, the principal anlage of postrenal V. cava has not appeared. In the later stages of Butler's highly interesting series of sheep embryos the large vessels ventral or medial to the mesonephros have disappeared, and the draining of the caudal region has been assumed by anlagen of postrenal Vv. cavae. Hochstetter had noted (1893) that the arrangement of veins in connection with the mesonephros of the sheep is atypical.

On pages 27–28, Stark (1835) further criticises Rathke:

> But ponder carefully the remarkable and very obscure transition in the course of which, according to Rathke, the right vein (*hintere Hohlvene*) is changed into the V. cava inferior in such a manner that one half, the upper half of this self-same vein, is disengaged from the spurious kidney and carried above its dorsal edge towards the aorta and between the Wolffian bodies, while the other, the posterior part, remains stationary on the upper edge of the spurious kidney. We need not fear that we shall diminish the credit of this farsighted Scholar, or injure his reputation, if we suspect that, in a matter so highly complex and where no one has had the opportunity of observing the series of changes from beginning to end, the V. cava inferior, which decreases in size from the liver caudally towards the kidneys and which goes to meet the veins which come from them, was thought by him to be the V. azygos, which gradually comes to naught in the region of the kidneys.

In Rathke's account I find no occasion for the inference of Stark that Rathke mistook the region of V. cava between liver and kidney to be a degenerating V. azygos. Consultation of Rathke's figures will afford conclusive evidence (see my figures 26 and 27; see also p. 194) that Stark was misinformed when he represented Rathke as claiming that the postrenal portion of his "hintere Hohlvene" remains stationary on the lateral side of the Wolffian body. The principal point of interest is this: Stark exhibited a healthy skepticism of "the obscure process of transition" by which a vein lying dorsolateral in the mesonephros extricates itself from that organ and comes to lie close to the aorta. In most eutherian mammals in which postrenal V. cava does not conform to the monotreme-marsupial type (for the latter type consult Hochstetter, 1893, *Tafel* 23, figures 27 and 28; 1896, *Tafel* 18; McClure, 1900; 1906-b; Tilney, 1912; Tribe, 1923) we have gradually come to recognize that the greater part of postrenal V. cava ordinarily arises from a circulation collateral to the posterior cardinal. In most cases these vessels coexist temporarily, separated from each other by the kidney. There remain certain mammals (the guinea pig and the rat) in which it is claimed that postrenal V. cava in its entirety is a remains of the original posterior cardinal line. This implies either that the posterior cardinal frees itself from intimate association with the Wolffian body, or (Butler, 1927, p. 330) that this association, which has never been very intimate (*ibid.*, figure 20-M), becomes even less so (*ibid.*, figure 22-O) as the permanent kidney effects a separation.

Views essentially similar to this have been held by Zumstein (1897) and by Begg (1917). The kidney is described as growing ventral and lateral to the posterior cardinal (consult Hochstetter, 1902, p. 143). From a certain amount of study of injected rat embryos I am convinced that the kidney of this animal remains medial to the main part of the lumbar posterior cardinal; that the latter vessel remains intimately associated with the Wolffian body and degenerates very rapidly as a collateral circulation is established medial to the kidney; that the vessels labelled *Pc.* in Butler's figure 22-O (1927) are not posterior cardinal veins, but rather that they are new vessels comparable to those described as "lumbar supracardinals" by the users of the latter term; that the postrenal posterior cardinal has degenerated partly or completely at the site of its original position in the mesonephros; that the correlation of mesonephric function and posterior cardinal persistence is not necessarily a negative one; that the indefinite enlargement of any or all elements of the "supracardinal plexus" of Butler's figure 21-N would fail to produce a vessel comparable to postrenal V. cava of any known mammal; that Stark's criticism of Rathke on the "obscure process of dissociation" of cardinal vein from mesonephros is applicable here. Future conflict of opinion upon the subject is most likely to be carried on between those observers who think that the history of V. cava can be worked out from reconstruction of a few stages of development, and those who believe it can not.

Stark and Kerschner had much in common. Each was fascinated by anomalous veins, and each sought to explain them largely by what he could find in the literature of his time. Each brought to light much valuable historical material. Neither did a great deal of embryological investigation. In the writings of either of these authors, one feels that here was a prelude to something tremendous which failed to materialize. On page 35, Stark makes this statement: "From the crural veins two new veins branch on either side towards the interior; these unite at the fifth lumbar vertebra to form a common trunk and constitute the newest part of the ascending V. cava, the part below the kidneys." He does not mention the source or age of any material studied in support of this statement. Kerschner derives postrenal V. cava from an "attenuated iliac vein."

The last statement ever made by Rathke upon mammalian veins occurs in the final sentence of the final chapter in his posthumous work in 1861. Here it is stated that the cranial-most segment of V. cava inferior is intrahepatic, and is derived from the omphalomesenteric vein. Stark had stated (1835, p. 27): "With his leave, I should be persuaded to think that our celebrated Authority took to be V. hepatica that which was V. azygos accessoria." (Consult my figure 20.)

THE HEPATIC CIRCULATION

From Rathke's account (1830-b) of the formation of the hepatic portal and the revehent hepatic veins, it is clear that he had made no pretence of following the history of those veins in his earlier work (1830-a). In his article (1830-b) devoted specifically to the hepatic circulation there is described (p. 437) a *Nabelvene*, the posthepatic portion of which in later stages is joined by a *Gekrösvene* to form the *Pfortader*. The vitelline and mesenteric veins are evidently described as forming the hepatic portal vein. The *Nabelvene* is described in early stages (p. 435) as having an uninterrupted course through the liver. It is said to join the transverse stem (duct of Cuvier of present usage) formed by the union of the "vordere und hintere Hohlvenen." That part of the *Nabelvene* joining the transverse stem is called V. hepatica (see my figure 20). On p. 436 (*ibid.*) he states that the middle part of the intrahepatic portion of the *Nabelvene* becomes constricted, so that its cranial part becomes revehent and its caudal part becomes advehent to the liver. He states that the cranial remnant is "die wahre V. hepatica" while the caudal remnant helps to form hepatic portal vein. He then describes anastomoses between the hepatic circulation and the right and left "halves of the *hintere Hohlvene.*" These are said to take place at the level of the cranial face of the liver. These anastomoses are said to form a new common stem which enters the V. cava. The cranial remnant of the *Nabelvene* is then said to degenerate. Thus a new hepatic vein is said to form. The description is very obscure. On page 436 he evidently describes the early formation of that part of V. cava lying in the caval mesentery: "zwei bis drei andere kleinere Gefässe, dagegen treten aus dem hintern Theile der rechten Hälfte der Leber hervor und münden sich in einer Reihe hinter einander in die Hohlvene ein." It is still possible to believe that Rathke's principal difficulty was one of terminology. If we are justified in believing that Rathke regarded the right posterior cardinal (of present usage) as transforming into V. cava in the cranial thoracic region, we may equally well accuse Stark of having believed that the entire lumbar region of that same vessel forms azygos vein.

There is reason to believe that Stark was not aware of Rathke's work (1830-b) on hepatic circulation. In the descriptions at that time no provision was made for a separate embryonic cardiac chamber, the sinus venosus. In the light of this fact, Rathke's description of hepatic part of V. cava as entering the common trunk of (what we now call) right anterior and posterior cardinal veins is a less serious error than Stark supposed.

The published record of the celebrated seminar given by Rathke (1838) is unillustrated. It is largely a mass of generalization often without specific mention of materials observed or sources of evidence. He described postrenal V. cava as taking its origin from the dorsal side of the venous stem connecting the hepatic part of V. cava with the renal anastomosis, and coursing caudally to the iliac region. He describes it as an unpaired structure. He does not state that it grows down from the liver. On this point, certain reviewers have misunderstood him. He states (p. 15) that the portion of V. cava behind the liver is formed in mammals "in ähnlicher Weise, wie bei den Vögeln." On pages 15–16 (concerning mammals) he states:

> Die erste Andeutung der Hohlvenen fand ich bei Schafembryonen, die 6½ Linien lang waren. Zuerst entsteht der Stamm, dann ein Paar Aeste, von denen ein jeder in dem innern Rande eines Wolffschen Körpers eine geraume Strecke nach hinten entlang lauft, und viele Zweige von diesem Organe, einen Zweig aber auch ganz vorne von der Niere empfangt. Darauf wachst der Stamm über seinen Theilungswinkel noch hinaus immer weiter fort, indem er nämlich einen unpaaren in der Okenschen Brücke nach hinten laufenden Ast absendet. Dieser schickt nahe dem hintern Ende der Wolffschen Körper, zwischen denen er liegt, an dieselben ein Paar Seitenäste ab, von denen von jeder ausserdem einen Zweig an den Hoden oder Eierstock seiner Seite abgiebt. Hinter diesen letztern Aesten aber bildet sich zwischen dem Ende jenes unpaaren Gefässes und demjenigen Theile einer jeden V. cardinalis, in welchen die V. cruralis und V. hypogastrica derselben Seitenhälfte übergehen, eine kurze Anastomose, die an der obern Seite des Wolffschen Körpers hinter der Niere ihre Lage hat. Wenn nun die Cardinalvenen und die Wolffschen Körper vergehen, wird diese Anastomose zur V. iliaca, das vor ihr liegende oder hintere Paar von Seitenästen der Hohlvene zu den V. renalibus.

Sabin and Butler have conclusively shown that in the ungulate mesonephros there develop ventro-medial venous paths collateral to V. cardinalis posterior which functionally replace the latter prior to the establishment of the anlage of postrenal V. cava. Since Rathke's study was made upon the sheep embryo, we may reasonably doubt whether he saw a "Veneninsel" similar to that seen by Hochstetter. It need scarcely be stated that he saw postrenal V. cava and V. hypogastrica coexistent.

In Rathke's account in 1838, he applies the term "Nabelvene" only to the umbilical vein and the term "Nabelgekrösvene" to the omphalomesenteric vein. His recognition of the adult derivatives of the allantoic and lateral line veins, and his interpretation of them in terms of the superficial abdominal veins in amphibians and reptiles are most instructive. He recounted these and several other phenomena for whose discovery Goette is usually given credit.

RATHKE'S TERMINOLOGY

Rathke's great contribution in 1838 was that of improved terminology. His *vordere Hohlvene* (1830) was changed by him (1838) to *V. jugularis*. His *hintere Hohlvene* became *V. cardinalis* The common stem of these two vessels (*Sinus veineux* of Cuvier, 1805; *truncus transversus* of von Baer, 1835) became *ductus Cuvieri*. To earlier embryologists it had been a source of pleasure to imagine that they beheld adult structures in early embryonic stages. The commendable practice of using strictly embryological terms for strictly embryonic structures was indulged in with caution. Yet here was a serviceable, non-committal term *cardinal* involving, we may believe, the concept *principal*. Until so recently as the writing of Kölliker's *Grundriss* (see my figure 1), Foster and Balfour's *Elements*, etc., the terminology of Rathke was that ordinarily employed. Then some one conceived the idea of calling Rathke's *V. jugularis* by the name *V. cardinalis anterior* ("anterior cardinal," "precardinal," etc.); also the *V. cardinalis* of Rathke became the *V. cardinalis posterior* (posterior cardinal, "postcardinal," etc.). There are now several varieties of *subcardinals* and *supracardinals*. Ductus Cuvieri is sometimes called *common cardinal*. Sabin (1917) uses the latter term most inappropriately in an account of the early posterior cardinal vessel. We have no objection, for instance, to the military titles: "major general" and "adjutant general." The title "corporal general" would neutralize the forces of the words involved.

Space does not permit of a discussion of the articles by Rathke upon birds, crocodiles, turtles, etc.

* * *

In the present account, no attempt will be made to review the recent and well-known contributions to the subject. I need only mention the familiar work of Huntington and McClure (1907 and 1920), in which it is concluded that the (non-posterior-cardinal portion of) V. azygos and the postrenal V. cava are serially homologous, developmentally continuous structures, derived from a single, simple, continuous, longitudinal, dextral embryonic vein called the "right supracardinal vein." This is not the complete statement of their views, but it represents the fundamental concept of their theory. I have already taken the liberty to suggest (1927) that in the typical eutherian mammal the postrenal V. cava has a temporary cranial serial homologue (located largely in the caudal half of the thorax) which never enters into the formation of the azygos vein; that there exists in the lumbar region a caudal serial homologue of (the non-posterior-cardinal-portion of) typical V. azygos which takes no part in the formation of postrenal V. cava. The suggestion has also been made by Reagan and Tribe (1927–28) that the present descriptions of the veins ventro-medial to the mesonephros are inadequate. It is not the purpose here to offer a review of the recent literature. This, however, may be said: whether we wish it or not, the formation of the V. cava is a much more complicated process than any existing account would indicate.

For the hospitality of the Department of Anatomy of University College, The University of London, I would express deepest appreciation. Access to the early nineteenth century collection which originally formed the libraries of Professor Sharpey and Professor Grant has been of great value, enabling me to secure for study a quantity of literature ordinarily unavailable. To Mr. F. Pittock, I am indebted for photographs of several original figures. Professor J. P. Hill and Dr. H. A. Harris have shown much interest in my efforts. Professors J. T. Wilson, G. Elliot Smith, and Arthur Robinson suggested many corrections of my original manuscript. The same is true of Dr. R. H. Hunter and Dr. R. J. Gladstone.

I regret that for the conservation of available space it has been necessary to indulge in very involved diction and an excess of parenthetical reference.

As one who is not a specialist upon the subject of V. cava, but merely as a reader interested in arriving at fundamental definitions of certain embryonic veins, I suppose I should apologize as a self-appointed reviewer of the subject. It was only after careful study of previous reviews that I felt justified in offering yet another. In no case have I meant to imply that independent rediscovery deserves less credit on point of originality than original discovery deserves. Doubtless there will be involved no unjustly unfavorable reflection upon the present era if we call to memory the work of those great masters of the science of Embryology, Heinrich Rathke and Karl Ernst von Baer. A knowledge of their remarkable achievements surely deserves to be perpetuated.

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RESPIRATION IN THE INSECTS

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ONE of the major problems that had to be solved successfully in the course of the evolution of terrestrial forms of life was that of obtaining an adequate exchange of gases to support metabolism, and at the same time of avoiding the danger of desiccation. Most of the other essentials for terrestrial life had already been developed by many of the aquatic forms of the Cambrian period. These essentials included some means of locomotion, a skeletal framework supporting the organs of the body and serving for the attachment of muscles, and a circulatory system providing for the distribution of food materials and oxygen. At the same time these forms were generalized enough in structure to be adapted, with but slight modifications, to conditions of life on the land or in the air.

Respiratory mechanisms of various types and degrees of complexity had also been developed in these aquatic forms. In the smaller ones with no horny exoskeleton a simple exchange of gases between the blood and the water through the whole body surface sufficed. In larger forms and in those possessing thick or hard protective coverings, gills of various types were developed. The respiratory problem was comparatively simple even for those animals that left the water for the habitat of the beach or the swamp. Their respiratory mechanisms were but little modified from those of their aquatic ancestors and must have been of tions as to require the frequent return to the water or the presence of much moisture.

In the course of time, however, respiratory mechanisms were developed which enabled their possessors to become independent of the shore and marsh and to range far inland, occupying even arid and desert habitats. It is of interest to survey briefly the existing groups of animals that have developed successful mechanisms for bringing thin, moist membranes into contact with the air, and at the same time preventing an excessive loss of water. The list is surprisingly small. It includes a few species of Protozoa, the Mycetozoa; a few nematode worms; the earthworms and the land leeches among the Annelida; one small group, the snails and slugs, of the Mollusca; a few crustaceans, the Onychophora, myriapods, insects and arachnids of the Arthropoda; and four groups of the Chordata, the amphibians, reptiles, birds and mammals.

Furthermore, all of the groups in the above list except some of the arthropods and some of the vertebrates have, strictly speaking, solved the respiratory problem by evading it—that is, by living in extremely limited and essentially semi-aquatic habitats. The Mycetozoa live on wet, decaying leaves. The earthworms and the terrestrial nematodes live in moist earth or in decaying organic matter. Here, with no other respiratory organs than their thin, moist skins they are able to lead a lethargic life with a comparadevelopment of an efficient respiratory pigment in the blood and of an excellent circulatory system has not saved the earthworm from the limitations which its thin skin has placed upon it. The pulmonate molluscs seek shade and dampness, although they can exist in comparatively dry habitats. The pulmonary sac which they have developed would not seem to be very efficient, although they probably do not require a very considerable respiratory exchange for their slow lethargic movements. It could hardly be said that any of these groups had met the problem of air breathing with conspicuous success.

The arthropods and the vertebrates present a different story. Both of these phyla have produced forms which have succeeded in adapting themselves to terrestrial conditions of all sorts—the arthropods through at least three separate lines of descent, and the vertebrates through one. Even within these two groups, however, widely varying degrees of success have been attained.

All five of the classes of the arthropods have terrestrial or semi-terrestrial representatives. Two of these classes are entirely terrestrial or have secondarily aquatic species. A number of the crustacea have established a semi-terrestrial existence on the strand and shore, and a few tropical crabs even climb trees and go far inland. Their physiological mechanisms, however, are still essentially those of aquatic animals. They seek moist or damp habitats when ashore and return to the water to breed. Some of the isopods, the pill- and sow-bugs, do not return to the water to reproduce, but their habitats, under stones and wood, are very limited. The myriapods, with a primitive tracheal system similar to that of the lower insects, are still not a particularly successful group of air breathing organisms. All of the arachnids except the oldest, the Xiphosuria, are terrestrial. Some of the spiders have developed tracheae of the simple sort, but the book lungs of the rest are not greatly modified from the book gills of the ancestral forms. The arachnids were handicapped in their attempt to solve the respiratory problem by a late origin from aquatic forms that were already highly specialized. In spite of that handicap some of them are, at present, able to exist under arid conditions. They are, however, not given to very energetic lives, although they may be capable of considerable activity in emergencies. Of all the terrestrial arthropods, only the insects have developed flying forms.

Among the land vertebrates there is an interesting parallel between the efficiency of the respiratory mechanisms and the activity and the success of the group. The lung fishes, the amphibia and the reptiles are able to live upon land, and possess lungs which provide for gas exchanges without danger of desiccation. But the only mechanisms for ventilating the lungs are the swallowing of air and the enlargement of the thorax by the action of the intercostal muscles and the ribs. Such actions are not particularly effective, especially during activity. All of these forms are comparatively much less active than the most of the mammals. Even the reptiles are lethargic creatures. For food, they mostly await what may come their way, and for protection from enemies they rely much, as do many of the arachnids, upon defensive armaments, disagreeable secretions, poison glands and the like, rather than upon energy consuming activities. Physiologically, the rate of absorption of oxygen may well be the limiting factor in determining the level of activity an organism may show. It is, of course, possible for an animal in an emergency to go into debt for oxygen, but the amount of such a debt is strictly limited, and the account must be settled promptly. In an organism which is able to meet only its ordinary demands, such a debt either could not be incurred, or would be repaid slowly with danger of collapse if another emergency should occur. It is quite possible that the large carnivorous reptiles of the late Mesozoic period were not as great a menace to the early mammals as they are commonly supposed to have been.

The mammals and the birds, on the other hand, have developed additional or accessory mechanisms for ventilating the lungs. The mammals have solved the problem successfully by dividing the ventral body cavity into two parts by the arched muscular diaphragm. The contraction of this muscle causes inspiration, and its passive return to the original position allows expiration. For the amount of energy expended, a much greater volume of air can be changed by such a mechanism than by the arching of the ribs by the intercostal muscles.

The birds have developed an extensive system of air sacs, in addition to their rather simple lungs. The bronchi communicate directly with nine large, thin-walled sacs, lying in the thorax and abdomen. At each inspiration nearly all of the air in the lungs is renewed, even when the bird is standing. During flight respiration is further assisted by the movements of the wings, and a still better ventilation is secured. The efficiency of the mechanism is indicated by the fact that the temperature of birds is usually higher than that of mammals, and also by the fact that flight, with a considerable energy expenditure, may be maintained for a long period of time. The flying insects show the same striking development of air sacs in the respiratory system as do the birds.

There are, then, only three groups of terrestrial animals that have developed highly successful respiratory mechanisms: the insects, birds and mammals. These three groups, furthermore, are energetic in their movements and are able to utilize continuously a large amount of energy in their muscular systems over a considerable period of time. The comparative activity and freedom of movement of all other terrestrial animals is slight. As for the insects, it is perhaps not an overstatement to affirm that, although other factors are undoubtedly involved, their signal success has been made possible by their adequately meeting the problem of providing a mechanism for gas exchange, sufficient not only for existence, but also for such energy consuming activities as rapid locomotion and flight.

THE STRUCTURE OF THE RESPIRATORY SYSTEM

Malpighi, in his monograph on the anatomy of the silkworm, published by the Royal Society of London in 1669, was apparently the first to show that insects respire by means of anastomosing tubes, branching to all parts of the body and connected with the exterior. Aristotle, on the basis of observations that insects are very resistant to asphyxia, had placed them in a group of animals which he called non-breathers. Aristotle had, of course, no knowledge of the essential nature of the process of respiration, and considered that the air served only to cool the vital spirits in the lungs. The non-breathing animals, presumably, had vital spirits so poorly calorific that there was no necessity of any special mechanism for cooling them. Malpighi in his monograph devoted several plates to the tracheal system and also described it in a number of other forms than the silkworm. Since his time the detailed structure of the system and its modifications have been described by many workers. Babak (1921) and Deegener (1913) have given excellent summaries of this and of the older physiological work, together with bibliographies.

The respiratory system in a typical perfect insect consists of a number of paired, segmental openings, the spiracles, and the tracheal tubes connected with them. The main tube leading from each spiracle soon divides into a number of large branches, some of which run longitudinally and unite with similar branches from the other main spiracular trunks. Other branches cross to the opposite side of the body and anastomose with the longitudinal trunks there. These main longitudinal and cross trunks give off a number of large branches, which in turn ramify everywhere inside of the exoskeleton, becoming smaller and smaller. Usually three large branches are given off in each segment from the main trunks; a dorsal branch to the dorsal muscles, a visceral branch to the alimentary canal and reproductive organs, and a ventral branch to the nerve ganglia and muscles. The head is especially well supplied by branches from the first spiracular trunk.

Every organ of the body is penetrated by a network of the smaller tracheal branches, which serve also the function of a connective tissue. True connective tissue is reduced to a minimum in the insects. The tracheae very largely take its place, anchoring the organs in place in the tube-like skeleton and holding together the elements composing the organs. The tracheoles are the terminal twigs of the respiratory tree. They are exceedingly slender tubes which arise from epithelial cells at the ends of the tracheal capillaries. They do not taper, have lumina less than one micron in diameter, and are unicellular in origin (Cajal, 1890; Holmgren, 1896). Anastomoses are common.

In structure the tracheae are homologous with the body wall. The same three layers are distinguished, the intima or chitinous cuticle, the hypodermis and the basement membrane. The intima, which is much thinner than the cuticle of the body wall, has one or more spiral thickenings, the taenidia, running the length of the tracheae. The taenidia extend to the tracheoles and play an important rôle in preventing the tubes from collapsing.

The Thysanura, considered the most primitive of the insects, show an interesting series of stages in the development of the respiratory system. One of the simplest forms, *Papirius*, has no tracheae at all (Lubbock, 1860). In another genus, *Machilis*, each spiracle supplies its own tracheal tree. There are no anastomoses of the branches from one spiracle with those from another (Lang, 1894). In other Thysanura, although the tracheal system is simple, both longitudinal and transverse anastomoses are present.

The spiracles, or stigmata, are arranged segmentally on the sides of the thorax and abdomen. Primitively there are twelve segments which may bear spiracles, but there is no known insect which has that number, and only one genus of the Thysanura, *Japyx*, which has eleven pairs. The most common number is ten pairs, two on the thorax and eight on the abdomen. In some of the higher insects there is a reduction in number to six or seven pairs, and some of the abdominal spiracles may migrate to the thoracic region. In the larvae of some forms with complete metamorphosis the number may be still further reduced. Other larvae have neither spiracles nor tracheae, either for a time after hatching or during their whole larval life. One genus of the Collembola, *Sminthurus*, is said to have a single pair of spiracles located on the head (Lubbock, 1860).

spiracular trunks immediately behind them are fitted with valves which can be opened or closed. In addition the stigmata are often protected by bristles or hair-like processes. The valves are of two kinds. In the external type the valvular apparatus is an integral part of the spiracle itself, and consists of the two spiracular lips. These are hinged and can be opened or closed by the action of muscles. Such spiracles are always found on the thorax and are larger than those of the second type. Internal valves are located just behind their spiracles on the tracheal trunks leading from them. In the larvae of some of the Diptera the internal valve is merely a sphincter muscle which by contraction occludes the trachea. Most of the higher insects, however, have a well developed apparatus whose construction and method of working was described by Landois (1867). A semicircular chitinous bow extends half way around the trachea. Between the ends of the bow extend a chitinous band and a lever with its muscles. The contraction of this muscle and the action of the lever stretches the bow nearly straight and compresses the trachea, whose elliptical passage is made slit-like. The relaxation of the muscle allows the trachea to open, supposedly by its own elasticity. These spiracular valves evidently serve some function in respiration, since all observers who have described them refer to their periodical opening and closing. In some insects they apparently make certain of the spiracles inspiratory in function by opening during the inspiratory movements of the abdomen and by closing during the expiratory movements. These actions will be further described below.

THE MECHANICS OF THE RESPIRATORY SYSTEM

No other phase of respiration in the insects has proved so puzzling as has the mechanism of the renewal of the air in the tracheal system, especially in the minute capillaries and tracheoles. This is partly because of the fact that a number of different physiological mechanisms, along with minor structural modifications, have been developed, sometimes within a single order. Aquatic forms have developed several different elaborate modifications of the system to serve for gas exchanges with the water. The matter is further complicated by the modifications which have been introduced in larval and pupal stages and in some nymphs. Often the mechanism in the immature form is quite different from that in the imago. Some idea of the very extensive literature on this subject may be given by the four hundred titles which Babak (1921) quotes in his review of the mechanics of the respiratory system in insects.

The simplest mechanism of gas exchange in the insects is that in a few Thysanura, in certain larvae that live in moist earth or in decaying organic matter, in the early stages of other larvae, and in some parasitic larvae. No tracheae are present in these forms (Palmen, 1877). The exchange of gases between the blood and the outer medium undoubtedly goes on directly through the thin integument. Such forms show but little activity, and presumably do not require a great amount of oxygen for their metabolic processes. A comparable condition is shown in the aquatic larva of *Chironomus*, in which the tracheal system apparently has little or no function in respiration. Hemoglobin is present in the blood of this form. Miall and Hammond (1900) state that the very rudimentary tracheal system appears only late in the larval stage. Fox (1921) investigated the localization of oxygen exchange in larvae of *Chironomus* by the use of the flagellate *Bodo sulcatus*. This protozoan migrates to a region having a certain optimum oxygen concentration, which is lower than that of ordinary water. Fox found that the larva absorbs oxygen by the whole body surface except the gills and the head. Micro-spectroscopic observations of the gills also failed to show oxidation of the hemoglobin there. It may be that the larva in its burrow makes more use of its gills than the above observations would indicate. It is difficult to see, however, that its tracheal system could be of any use whatever in respiration.

The next degree of complexity of the mechanism is that exhibited by most larvae, by pupae, and by some small imaginal forms, in which respiratory movements are lacking. True respiratory movements are also absent in the Arachnida and the Myriapoda. Diffusion alone, through the open spiracles and the tracheal tubes, must serve in these instances. Krogh (1920) has shown that the wood boring larvae of *Cossus*, a moth, exhibit no true respiratory movements, and has demonstrated directly that an adequate diffusion of oxygen into the tracheal system occurs. Over one spiracle was placed a short tube connected to a second horizontal tube in which a drop of oil served as an index of volume. The drop of oil showed a steady movement toward the spiracle due to a diminution of the enclosed quantity of air as a result of the oxygen consumption in the animal.

RESPIRATORY MOVEMENTS

In most of the insects, and especially in those with well developed powers of flight, the ventilation of the system is assisted by rhythmical movements of the abdomen. Plateau (1884) has given us the classical description of the movements in many insects. He placed the living insect in a stereopticon lantern and traced the outlines of the enlarged shadow on a screen. In general, the inspiratory movements consist of the expansion of the abdomen. The movements of the head and thorax which may sometimes be observed in some insects are probably only passive and are the results of pressure changes. The expiratory movements consist of the contraction of the abdomen either vertically or transversely. In the Aculeate Hymenoptera longitudinal movements of the abdomen occur together with vertical movements. The vertical movements are always present, and are the more effective. The expansion and contraction of the abdomen are associated with an increase and decrease in the volume of the abdominal cavity. Each abdominal segment is composed of a large tergal or dorsal plate, covering the ventral surface. In some forms the sternum covers more of the sides than does the tergum, and in other forms the two cover the sides about equally. A flexible pleural membrane connects the edges of the tergum and sternum. The terga bear the spiracles in the lower anterior margin. In some insects, such as the Coleoptera, Hemiptera and Blattidae, the rigid sterna yield but little, and the greater movements are made by the thinner terga. In the Odonata, Diptera, Hymenoptera and Acrididae of the Orthoptera, the terga are better developed and fit over the sterna like the lid of a box. Most of the movement is allowed by the membranes, which fold in at contraction and straighten out at expansion. In the Lepidoptera, Neuroptera and Locustidae of the Orthoptera, there is a space between the sterna and terga that is closed by the pleural membranes. At expiration the sterna and terga approach each other, folding the pleura.

It was formerly held that only the expiratory movements are caused by muscular contraction. Inspiration was supposed to be purely passive, caused by the elasticity of the body wall. It is possible that in some insects, such as the cockroach, the elasticity of the distorted chitinous arcs would cause them to return to their original shape. In many insects, however, it can easily be observed that no such distortion occurs. It is now known that in the Hymenoptera, Diptera, Trichoptera and many of the Orthoptera, inspiratory muscles are present. In the grasshopper, for example, on either side of the sternum of each abdominal segment, an apodeme, or chitinous projection, extends up into the abdominal cavity. Muscles extend from the distal or dorsal end of this apodeme to the ventral edge of the corresponding tergum. Contraction of these muscles separates the sterna and terga, and enlarges the abdominal cavity.

It seems altogether likely that inspiratory muscles will be found in many other groups. In some of the aquatic beetles and Hemiptera, for example, which are known to exhibit respiratory movements, it would appear impossible for inspiration to occur against the hydrostatic pressure without active muscular exertion. It also seems impossible for the nymphs of Anisopterid dragonflies to take a sufficient quantity of water into the rectum merely by passive expansion. Further, there is a physico-chemical objection to the idea that the gas in the tracheal system is compressed by the contraction of the abdomen, and that it causes the passive expansion of the abdomen when the muscles relax. The air in the tracheal system must be at all times under a pressure not much different from atmospheric, since the tensions of the gases dissolved in the water are in equilibrium with the partial pressures of the atmosphere. If the pressure of the air in the tracheal system were greater than the tension of the dissolved air, the system would lose gas through the gills, rather than gain it. The hydrostatic pressure on the outside of the abdomen tending to collapse it is considerable, since the larvae may live at a depth of five meters (Muttkowski, 1918). It is difficult to imagine how the abdomen could enlarge passively without muscular effort against such a hydrostatic pressure. According to Tillyard (1917) the respiratory movements are vigorous and a large volume of water is drawn in rather quickly.

THE RENEWAL OF THE TRACHEAL AIR

The older idea of the ventilation of the tracheal system was that a tidal inflow and outflow of air through all of the spiracles occurred. Landois (1867) believed that there was an injection of air into the finest tracheal branches by pressure caused by the contraction of the abdomen and the simultaneous closing of all of the spiracular outlets of the system. The physical impossibilities of such a mechanism are obvious, and the explanation was never generally accepted. In a number of insects a sort of circulation of air through parts of the tracheal system has been demonstrated. Certain spiracles, as a result of their valvular actions, function normally only for inspiration and others only for expiration. Brocher (1909, 1911, 1912) has shown that in the Dytiscidae the seventh and especially the eighth pairs of abdominal spiracles are inspiratory, while the other six abdominal pairs serve chiefly for expiration. In the Notonectidae, only the last pair of spiracles are inspiratory. In *Hydrophilus*, according to Brocher, all of the abdominal spiracles are inspiratory except the last pair, which are expiratory. In the Orthoptera, the two pairs of thoracic and the first one or two pairs of abdominal spiracles open during the inspiratory phase of respiration, and close during the expiratory phase (Lee, 1925). The last six pairs of abdominal spiracles are open during expiration and closed during inspiration. Most of the expired air comes from the last or tenth pair of spiracles. The air thus traverses the longitudinal tracheal trunks from the thorax to the end of the abdomen. The mechanism may be easily demonstrated and expired air collected by thrusting the abdomen of the insect through a hole in a piece of rubber dam covering the mouth of a vial filled with a suitable liquid, and allowing the expired air to displace the liquid. In *Dixippus*, a European species of the Phasmidae or walking sticks, Buddenbrock and Rohr (1923) found that the thoracic spiracles open during expiration and close during inspiration, thus, apparently, allowing a circulation of air from behind forwards. In another Phasmid, *Diapheromera femorata*, the opposite action has been found (Lee, 1927), the thoracic spiracles being normally inspiratory in function. It may be that the action is different in the two species, or the difference may be due to the fact that Buddenbrock and Rohr used partially asphyxiated animals. The normal respiratory movements of *Dixippus* were so slight that they placed the animal under water for a few minutes in order to obtain dyspneic movements. It is altogether likely that under such conditions the normal action of the spiracular valves might be changed.

Such a circulation of air as that just described could, at the most, serve to ventilate only the main longitudinal and cross trunks of the tracheal system. For the renewal of the gases in the smaller tracheae and in the capillaries and tracheoles other mechanisms must be sought. It is probable that the process of diffusion, or a combination of this process with the action of the air sacs, provides an adequate explanation of the ventilation of even the remotest parts of the tracheal tree. Winterstein (1921) has expressed doubts as to the possibility of diffusion through the long, narrow and tortuous tracheal tubes being able to suppy an adequate amount of oxygen, especially during activity. He says (pp. 111–112):

> Wenn man bedenkt, dasz trotz einer relativ vollkommenen Atmungsmechanik in einen Organ von leicht und ausgiebig veränderlichem Volumen, wie es die Säugetierlunge ist, die Alveolarluft sich sowohl in ihrem Sauerstoff- wie in ihrem Kohlensäuregehalt um mehrere Prozent von dem der äuszeren Luft unterscheidet, dann erscheint es kaum faszbar, wie auch durch sehr ausgiebige Atembewegungen in einem System dünner und ziemlich starrer Röhren, deren feinste Ausläufer an der Grenze des mikroskopisch Wahrnehmbaren liegen, eine genügende Erneuerung des Gasinhaltes bewirkt werden kann.

Krogh (1920) has stated his position thus:

> Die chitinösen Tracheen . . . . . sind gewöhnlich von zirkulärem Querschnitt und mit einer spiraligen Verstärkungsleiste—dem Spiralfaden—ausgestattet. Durch diese Struktur wie im allgemeinen durch ihre kleinen Dimensionen setzen die Tracheendem Zusammenpressen durch Druck einen sehr bedeutenden Widerstand entgegen, und eine einigermassen ausgiebige mechanische Ventilation des Tracheensystems wird offenbar schwerlich zustande kommen. Andererseits ist es sehr schwer einzusehen, wie eine unvollständige Kompression des Tracheensystems eine Erneuerung der Luft in den feinen Endzweigen bewirken könnte, und man muss zugeben, dass eine befriedigende Erklärung des Respirationsmechanismus der Tracheaten bisher fehlt.

The theoretical difficulties of diffusion alone serving to supply oxygen to the tracheal end branches led Krogh to put the problem to experimental test. He was able to show that in a number of forms, when at rest, diffusion was able to furnish an adequate supply of oxygen to the tissues. Krogh (1913) first made a study of the composition of the gases in the tracheae of the jumping legs of the grasshopper, in order to determine the rapidity and completeness of the exchange of gases in these tracheae with the outside air. A leg was clamped off close to the body, removed and submerged in glycerine. A bubble of gas from the tracheae of the leg was then forced out into the glycerine and analyzed. The legs of other grasshoppers that had been fatigued to exhaustion were treated in the same way. The average results, corrected for systematic experimental errors, were as follows:

	Resting per cent	*Fatigued per cent*
CO_2	2.5	5.0
O_2	15.5	5.0
N_2	82.0	90.0
Apparent R.Q.	0.4	0.26

Since in both the resting and the fatigued legs the carbon dioxide content of the tracheal gas was much less than the oxygen deficit, it must be that a considerable proportion of the carbon dioxide is carried away by the blood, in which it is freely soluble. This is, of course, on the justifiable assumption that the apparent respiratory quotient is much lower than the true metabolic one.

Krogh next placed grasshoppers in an atmosphere containing only oxygen and carbon dioxide, until no nitrogen remained in the tracheae. The animals were then removed to ordinary air and the length of time determined for the normal nitrogen content of the tracheae to be restored. After only one second there was 2.5 per cent of nitrogen in the tracheae, and after only fifteen seconds, or nine respirations, there was 60 per cent. Restoration was complete within one minute. Krogh estimates that about 20 per cent of the air in the leg is replaced by pure atmospheric air at each respiration. This would indicate that the combination of respiratory movements and diffusion is surprisingly efficient in rapidly ventilating even the very small tracheal branches. Analyses of gases from the hind legs of locusts, scarab beetles and ground beetles indicated a close parallel between the efficiency of the respiratory mechanisms and the amount of activity ordinarily manifested by the animal.

Krogh (1920) has further investigated the factors affecting diffusion, using forms (larvae of *Cossus* and *Aeschna*) in which mechanical ventilation of the tracheae could play no part. At the inner ends of the tracheal tubes, where the absorption of oxygen is going on, there will be a partial pressure of that gas less than its partial pressure in the atmosphere. As a result of this difference in tension, oxygen will diffuse inwards. The amount (S) which will move in per second will be proportional to the difference in the oxygen partial pressures in the atmosphere and tracheoles ($p - p_1$), and to the cross section area (A), and inversely proportional to the tube length (L). Or,

$$S = k\,\frac{(p - p_1)\,A}{L}$$

k is the proportionality constant, which for oxygen and ordinary temperature is about 0.18 for the selected units. Krogh made the necessary measurements of the oxygen consumption per second, S, the cross section area of the tracheae, A, and their average length, L. The difference in pressure, ($p - p_1$), necessary for the diffusion could then be calculated. This difference in pressure was found to be 0.13 per cent of an atmosphere for the myriapod *Scutigera*, 2.2 per cent in *Tenebrio* larvae, 2 per cent in *Cossus* larvae, 1.7 per cent in *Lasiocampa* larvae, and 6.2 per cent in *Aeschna* nymphs. Krogh then measured, in an ingenious way, the actual oxygen tension within the tracheal system in *Cossus* larvae. A few spiracles were left exposed to the air and small bells of collodion were sealed over the others. After a sufficient period of time for equilibrium, the gas in the bells should be of the same composition as that in the tracheal system. Analyses of this gas showed oxygen tensions lower than the oxygen tension of the atmosphere by amounts in very close agreement with those calculated by the above formula.

By the use of Krogh's microrespiration methods, Buddenbrock and Rohr (1923) showed that the closure of all of the spiracular openings in *Dixippus* reduces the respiratory exchange about three-fourths. The gas exchange directly through the integument in this form is thus about one-fourth of the ordinary resting rate. The oxygen tension of the tissues was found to be about 10 per cent of an atmosphere. The reduction of the oxygen content of the air down to 10 per cent had no effect, as would be expected. Below this concentration of oxygen the respiratory movements increased in frequency and amplitude.

It would appear to have been conclusively demonstrated that the process of diffusion alone is sufficient for an adequate gas exchange in the great majority of larvae, all pupae, and in the smaller and comparatively lethargic adult insects. In the larger, more active forms, and especially in those with well developed powers of flight, the process of diffusion alone must be inadequate. Krogh himself has pointed out, that as the size of the insect increases, diffusion remains proportional to the linear dimensions, while weight increases as the cube of the linear dimension, and the resting oxygen consumption increases at a rate between the square and the cube of the linear dimension. The oxygen consumption of the higher insects, even when at rest, is much above that of the less active smaller forms. In the honey bee an oxygen consumption of 20,000 cc. per kilogram per hour has been observed (Parhon, 1909). During flight the oxygen consumption must be much greater than this. For such a consumption diffusion alone will not suffice, as Krogh has emphasized, even if the body weight is only 0.1 gram. In this connection a possible function of the air sacs may be considered.

THE AIR SACS

Air sacs are found in most of the winged insects, and in many of the non-flying forms. They are simple, elastic, epithelial-lined dilatations of the tracheae, usually without the intimal layer. They vary greatly in size, number and distribution in the various groups. In fact, they show a parallel development with the powers of flight and in some of the most successful of the flying insects they may together occupy as much space as the alimentary canal. It is not generally realized how great their number may be in an insect. Landois (1867) states that the number in the male of *Melolontha vulgaris* is around 550, many of which approach a diameter of 2 mm. Alt (1912) has described the veritable complex of air sacs in the thorax and abdomen of *Dytiscus marginalis*. Packard (1878) has counted fifty-three sacs in the head alone of *Melanoplus femur-rubrum*. Vinal (1919) has described the extensive air-sac system of the Carolina locust, *Dissosteira*, and his illustrations show small air sacs in the large jumping legs. According to Newport (1851) there are air sacs even in the mandibles of the stag beetle. It is especially noteworthy, in view of their possible function, that many of the sacs arise from the smaller tracheal branches at a considerable distance from any spiracles. Even the largest ones do not open immediately off of the large spiracular trunks, but usually from some of the longitudinal trunks. They are located all through the body, the large ones usually directly beneath the hypodermis, while the smaller ones may be buried among the muscles. Miall (1903) has described dilatations in the tracheae of the larva of *Ptychoptera* which can be expanded like air sacs and MacGillivray (1903) has described air reservoirs in the aquatic larva of *Donacia*. The sacs are not blind pockets at the ends of tracheal tubes, but usually have many efferent branches, which are very short as compared with the total length of the tracheal tree.

Up to the present time, the functions of the air sacs have been far from convincingly described. Two different functions have been ascribed to them. Newport (1851) observed their number and size in the rapidly flying insects, and was led to the naïve belief that they serve for buoyancy during flight by lessening the specific gravity of the body. Newport believed that the air sacs in the birds serve the same function. It is of course true that the specific gravity with respect to water, of the body as a whole would be lessened, but the weight to be supported by the wings would be just as great whatever the expansion of the body, and the greater air resistance and unwieldiness of the larger bulk would be a disadvantage. It is quite possible that the air within the sacs is at slightly higher temperature than the outside air, but the buoyant effect from such a cause would be inconsiderable. It is possible that an increased size of skeleton may be advantageous for the attachment of muscles. Larger flies, for example, have greater powers of flight than do the small ones. It is certainly true that in the birds the respiratory function of the air sacs in ventilating the lungs is by far their most important one.

The other view which has been held regarding the function of the air sacs is that they are simply reservoirs of air, especially developed in the flying insects because these forms consume a great deal of oxygen in flight. There are a number of reasons for rejecting such a simple explanation. There would seem to be no advantage to an insect in having air reservoirs within the body when the whole atmosphere is a reservoir just a few millimeters away through the open spiracles. The amount of air in the sacs could hardly serve as a source of oxygen for very long, unless constantly renewed, since the total volume of the sacs is small compared with the volume of air the animal uses in an hour, and less than 20 per cent of the gas is oxygen. If the functions of the sacs were either for buoyancy or as a reservoir there would seem to be little reason for having 550 small sacs, as is the case in *Melolontha*, rather than a few large ones.

It would appear that another explanation, almost self-evident, would account not only for the presence of the air sacs, but for their parallel development with the powers of flight. This explanation is that their function is chiefly mechanical, in allowing a considerable volume of air to be inhaled and exhaled (Lee, 1928). The mechanism will be made clear if one imagines the body of an insect as containing no air sacs at all. The ordinary tracheae offer considerable resistance to pressure tending to collapse them. Neither can they be distended to any appreciable extent. They are elastic only in that if they are distorted out of round by pressure they will return to their original shape when the pressure is removed. The spiral taenidial threads would appear to be especially effective in preventing either collapse or distension. The cavities of the insect's body have no connection with the lumen of the tracheae, Therefore, in such an insect without air sacs, both the inspiration and expiration of air would be absolutely impossible.

With air sacs present, whether a few large ones or many small ones, the situation is entirely different. In so far as the mechanics of respiration are concerned, the insect could be compared in a number of respects with the bird or mammal. The hemocoele of the insect would be analogous with the whole body cavity of the bird or the thoracic cavity of the mammal. The active expansion of the abdomen of the insect would be analogous with the increase in size of the body cavity in the bird or of the thoracic cavity in the mammals. During the expansion of the abdomen the hemocoele becomes larger and the intracoelomic pressure must decrease. As soon as this intracoelomic pressure becomes less than atmospheric, the air, having free access to the tracheal system through the spiracles, will dilate and fill the thin walled elastic air sacs, wherever they are located. During expiration, the abdomen is compressed and made smaller, the intracoelomic pressure is increased above atmospheric, and this pressure, transmitted by the blood to all parts of the body, will cause the air sacs to collapse and empty themselves. The greater the total capacity of the air sacs, the greater would be the possible ventilation in a single respiration. The pressure causing the alternate dilatation and collapse of the air sacs is first the pressure of the outside atmosphere and then the blood or intracoelomic pressure.

If such a conception of the function of the air sacs is correct, there would be an enormous advantage in having a great number of small air sacs scattered throughout the body, rather than a few large ones. Each sac would serve to ventilate the section of tracheal tube between it and the nearest open spiracle. The agitation given to the tortuous column of air should be very effective indeed in aiding the diffusion of oxygen. It has long been a puzzling question how the organs in the head of an insect, far removed from the spiracles, could get by diffusion enough oxygen to supply their needs. With this view of the function of the air sacs the difficulty disappears. The changes in intracoelomic pressure will be transmitted by the blood to the air sacs of the head as well as to any others, and cause the alternate collapse and dilatation. The work of Krogh, reviewed above, would indicate that for the comparatively short distance between the air sacs and the terminal tracheal capillaries, the process of diffusion alone would supply an adequate amount of oxygen for the needs of even the most active insects. The parallel development of the air-sac system with the powers of flight would indicate the efficiency of the mechanism for supplying an adequate gas exchange for such an energy consuming activity.

Such a view of the respiratory action of the air sacs implies that inspiration is an active muscular act. During inspiration there must be a decrease in the intracoelomic pressure to below atmospheric for any distension of the air sacs to occur. It is difficult to see how the abdomen could expand passively against a positive atmospheric pressure. The presence of inspiratory muscles in a number of groups has been noted above. Such muscles may be found in other groups, or the elasticity of the chitinous arcs of the abdominal wall, distorted during expiration, may be great enough to cause, in returning to their original shape, a partial vacuum in the abdomen.

The changes of pressure in the air sacs of the grasshopper, *Melanoplus differentialis*, may easily be demonstrated by watching the sacs through the transparent conjunctivae under the wings on the mesonotum and metanotum. The wings should be pulled back or cut away. At each contraction of the abdomen the thin conjunctivae will be seen to distend and the air sacs beneath them may be seen, dilated at first, then gradually emptying. Upon the expansion of the abdomen or during inspiration the conjunctivae will be seen to be pressed inwards by the atmospheric pressure, and the air sacs may be seen to dilate and fill at the same time.

THE LOSS OF CARBON DIOXIDE

The elimination of the carbon dioxide produced in the body of the insect is less difficult of explanation than is the supplying of oxygen. Any mechanism which adequately explains the renewal of the oxygen supply in the capillaries and tracheoles will also account for the loss of carbon dioxide. Numerous analyses of the air expired from the tracheal system in various insects have shown that the carbon dioxide content is from two to five per cent. Although in many cases this amount is considerably less than the oxygen deficit, it is undoubtedly true that the greatest part of the carbon dioxide exchange is by way of the tracheae. Accessory mechanisms, however, may account for a significant part of the total loss. Buddenbrock and Rohr (1923) state that about one-fourth of the ordinary gas exchange in *Dixippus* occurs directly through the integument. It has been suggested that in ecdysis, especially at the end of pupation, accumulated carbon dioxide is lost, both as carbonate in the old skeleton and as gas directly through the new soft chitin.

RESPIRATORY PIGMENTS

The respiratory pigments hemocyanin, hemoglobin, chlorocruorin and others have been found in the blood of many of the invertebrates, and it has been thought that the blood of the insects might contain some such chromoprotein. The larvae of some of the harlequin flies, Chironomidae, were shown by Rollett (1861) and Lankester (1873) to have hemoglobin in their blood. These larvae often live under more or less anaerobic conditions, such as are found in the deeper waters of lakes and in thermal springs (Brues, 1927). Miall and Hammond (1900) considered that the hemoglobin in the larva of *Chironomus* is employed as a store for oxygen, rather than as a transport mechanism. Leitch (1916) has shown that such a view is untenable. The quiet larva uses about 2.675 milligrams of oxygen per gram of body weight per minute. At such a rate of consumption the hemoglobin could serve as a store of oxygen for a maximum of about twelve minutes, rather than for several days as Miall thought. According to Leitch the larvae do not utilize their hemoglobin unless the oxygen tension of the water is below seven millimeters. At tensions above this the oxygen in physical solution in the blood is sufficient for the needs of the body and is renewed rapidly enough from the water that the hemoglobin does not dissociate. She believes that the function of the hemoglobin consists in making available by its power of binding oxygen chemically, a quantity of oxygen sufficient for the needs of the larva, at oxygen tensions so low that the necessary amount is not supplied by physical solution.

Muttkowski (1921) has shown the presence of copper in the blood of all of the insects he studied, thirty-four species, representing all of the chief orders. Quantitative determinations were not made. The tests indicated, however, that the copper was present in amounts comparable to that in crayfish blood.

In many of the Crustacea copper has been shown to be the nucleus of the respiratory pigment hemocyanin. Muttkowski believes that the copper in insects' blood is similarly a part of a respiratory pigment and that the blood of an insect has a respiratory function strictly comparable to that of the blood of the vertebrates. The presence of such a chromoprotein would help to explain the apparent efficiency of the blood gills found in a number of aquatic forms. The problem is an interesting and important one, and it would appear well worth while to put on an experimental and quantitative basis the possible rôle of copper in a respiratory pigment in insect blood. As to the properties of hemocyanin and the nature of its union with oxygen, there have been many conflicting reports. In a late careful investigation Redfield, Coolidge and Hard (1926) have demonstrated that the hemocyanins of four marine invertebrates, *Limulus*, *Loligo*, *Busycon*, and *Cancer*, function in the transport of oxygen and carbon dioxide according to the same physico-chemical principles as obtain in the case of hemoglobin.

THE CONTROL OF RESPIRATION

Bethe (1897) and Ewing (1904) have studied the nervous control of respiration in some of the insects. In the Orthoptera, and probably in most of the higher insects, each ventral ganglion of the abdominal chain is the center for the respiratory movements of its segment. Respiration continues after decapitation, and sections of the abdomen of only one or two segments will exhibit respiratory movements for some time. Each ganglion also controls the movements of the spiracular valves in the segment to which it belongs. Ewing removed the thoracic ganglia of grasshoppers and found that the thoracic spiracles were paralyzed. Faivre (1875) thought that the thoracic ganglia were the only respiratory centers in *Dytiscus*, but this work has not been confirmed.

In addition to this segmental arrangement there obviously must be an additional or supplementary mechanism for the correlation of the movements of the various segments. This is especially true for the movements of the spiracular valves in the forms in which they are opposite in action in the thorax and abdomen. It would seem that the question of both nervous and chemical control of respiration in insects would well repay further extended investigation.

Carbon dioxide is a specific stimulus to the respiratory center in the mammals. It is doubtful whether it is such a stimulus to the centers in the insects. Babak and Foustka (1907) consider that oxygen lack in some way causes stimuli promoting respiratory movements in dragonfly nymphs. They found that if the water were very poor in oxygen, a typical dyspnea appeared. In water saturated with oxygen and covered with an atmosphere of pure oxygen, long periods of apnea occurred. Changes in the concentration of carbon dioxide had no such effect upon the respiratory rhythm. Buddenbrock and Rohr (1923) observed that when the oxygen content of the air was reduced to 3 or 4 per cent, the respiratory movements of *Dixippus*, which are ordinarily very slight, become energetic.

RESPIRATION IN AQUATIC FORMS

Complicated as is the mechanism of respiration in the insects, it is still more complex in the many aquatic forms. Here mechanisms originally developed for air respiration on land, have been secondarily modified to function in water. So far as is known all water inhabiting insects are descended from terrestrial forms and are only secondarily aquatic.

The number of species that have taken up life in the water is surprisingly large. If permanent adaptations to all sorts of environments be one measure of biological success, then the insects must be placed above all other groups in this respect. It is probable that in several orders a number of separate changes to aquatic life have been made and quite different mechanisms for gas exchange have been developed. There are, too, all degrees in the completeness and efficacy of the modifications for respiration. In the aquatic environment there are many different habitats involving very different conditions of oxygen supply. Some habitats are almost lacking in oxygen; in others the oxygen tension, due to green water plants, is greater than the oxygen tension of the atmosphere. Insects may be found under almost all of these conditions, wherever food may be found.

The holopneustic forms, or those with open functional spiracles, are wholly or partially independent of the dissolved oxygen of the water. They breathe at the surface, carry a supply of air below with them or utilize the air stores in the stems or leaves of water plants. As might be expected, their respiratory mechanisms are essentially the same as those of terrestrial forms. In aquatic insects which have an apneustic or closed spiracle system, but which depend upon the tracheal system for the distribution of oxygen from the gills to the tissues, the bodily movements can probably be of little or no aid in helping the mixing of the gas within the tracheae. The tracheal gas must be under approximately atmospheric pressure, or less, since it is in equilibrium with the gas dissolved in the water. The actual pressure on the tracheal tubes tending to collapse them, however, may be considerably more than atmospheric. Dragonfly nymphs, for example, may live at a depth of 4 to 5 meters. The total outside pressure may thus be upwards of 1.4 atmospheres. The tracheal tubes must be able to withstand such a pressure without transmitting it to their contained air. Otherwise there would be a steady loss of the gas through the gills to the water and the end result would be the complete emptying and collapse of the tracheae.

The following table lists the more common forms of aquatic insects, and the mechanisms used for gas exchange in each case.

The work on the respiratory mechanisms in the larvae of the Odonata has been reviewed by Tillyard (1917). Most of these larvae are carnivorous and predacious and show considerable activity in the water. They are found in a wide range of habitats, varying from swiftly running water to swamps and bogs, and from shallow water to deep. In the larvae of the Anisoptera, the anterior two thirds of the rectum is expanded into a barrel-like chamber, the branchial basket. From the walls of this chamber six longitudinal sets of gills project into the lumen. Each gill is abundantly supplied with tracheal branches and capillaries and from 10,000 to 90,000 tracheolar loops. By the respiratory movements of the abdomen, water is alternately drawn into and expelled from the rectum. According to Krogh (1920) the nymph of *Aeschna* consumes about 300 cc. of oxygen per kilogram per hour, an amount which can easily be supplied by diffusion from the water into the tracheal system and to the tissues.

In the Zygopterid larvae, the caudal and lateral tracheal gills are waved to and fro in the water and probably serve for gas exchange. If these gills are lost, however, the larva is still able to live. The rectum presumably serves also for respira-

COMMON AQUATIC INSECTS

GROUP	AQUATIC STAGE	METHOD OF RESPIRATION
Odonata	Nymphs of all species	
Anisoptera		Tracheal gills in anterior portion of rectum.
Zygoptera		Caudal tracheal gills in most. In some, lateral tracheal abdominal gills. Blood gills in rectum.
Trichoptera	Nymphs of all species	Lateral abdominal tracheal gills. Blood gills in some.
Ephemerida	Nymphs of all species	At first through integument only; later by lateral tracheal gills, usually on abdomen only but on thorax in some forms. Rectal blood gills.
Plecoptera	Larvae of all species	Caudal tracheal gills in most forms. Thoracic tracheal gills in a few.
	A few adults	Caudal tracheal gills much like those of the larva.
Neuroptera		
Hemerobidae	Larvae	Caudal tracheal gills.
Sialidae	Larvae	Lateral abdominal tracheal gills.
Corydalidae	Larvae	Lateral abdominal tracheal gills.
Hemiptera		
Corixidae	Nymphs and adults	Air breathing at surface. Air store carried below by hydrofuge hairs.
Nepidae	Nymphs and adults	Air breathing through long tubes at end of abdomen.
Notonectidae	Nymphs and adults	Air breathing at surface. Air film around body when submerged.
Belostomidae	Nymphs and adults	Air breathing. Tip of abdomen thrust through surface. Floats head downwards.
Coleoptera		
Hydrophilidae	Larvae	Spiracles at tip of abdomen.
	Adults	Air space between elytra and abdomen. Also air film under abdomen.
Gyrinidae	Larvae	Lateral and caudal tracheal gills.
	Adults	Air bubble carried at tip of abdomen when submerged.
Dytiscidae	Larvae	Air breathing by two spiracles at tip of abdomen.
	Adults	Air store between elytra and abdomen.
Hydrobius	Larvae	Spiracles at end of abdomen; air bubble carried below surface; short lateral gills.
	Adults	Air store under elytra and film of air around abdomen.
Chrysomelidae		
Donacia	Larvae	Spines, which are thrust into air cavities of water plants, form a tube through which air is obtained.
Haemonia	Adults	Air stores around abdomen.
Pelobius	Larvae	Lateral abdominal blood gills.
Haliplidae	Adults	Air stores around abdomen.
Lepidoptera		
Nymphula	Larvae	Through integument only in some; by tracheal gill filaments in some; in others by combination tracheal-blood gills.
Cataclysta	Larvae	Blood gills.
Hymenoptera	Larvae of a few small parasitic forms	Directly through integument.

GROUP	AQUATIC STAGE	METHOD OF RESPIRATION
Diptera		
Psychodidae	Some larvae	Caudal tracheal gills; caudal spiracles; air bubble carried below surface.
Corethridae	Larvae	Through integument. Imperfect tracheal system.
	Pupae	Respiratory tubes from head to surface of water.
Chironomidae	Larvae	Through integument: hemoglobin in blood.
	Pupae	Respiratory filaments from prothorax.
Blepharoceridae	Larvae	Ventral abdominal tracheal gills.
Culicidae	Larvae	Respiratory tube from end of abdomen to surface. Also rectal respiration.
	Pupae	Two respiratory tubes from back of thorax. Hangs from surface film.
Stratiomyidae	Larvae	Spiracles at end of elongated abdomen. Hangs from surface film.
	Pupae	Floats on surface of water.
Tipulidae	Some larvae	Through integument.
Syrphidae	Larvae	Long caudal tube to surface.
Simulidae	Larvae	Respiratory filaments from head. Lives in swiftly flowing streams.
	Pupae	Respiratory filaments from head.
Dixidae	Larvae	Spiracles at tip of abdomen, which is thrust through surface film.
	Pupae	Respiratory tubes on thorax.

tion, although it contains no true tracheal gills. The same situation exists in the Ephemerida, the lateral tracheal gills being supplemented by the rectum.

It is generally agreed that Odonate larvae were once air breathing forms (Dewitz, 1890). Krogh (1920) considers it most likely that the nymphs of the enormous dragonflies of Carboniferous time must have had an open tracheal system and mechanical respiration. The adults were approximately 30 cms. long and 0.3 cms. wide. Krogh has calculated that diffusion alone could not possibly supply enough oxygen in such large forms.

Little is known of the physiology of respiration in the aquatic larvae of the Trichoptera, Plecoptera, Megaloptera and Neuroptera. All of these forms possess tracheal gills, either lateral or caudal. It is inferred that gas exchange takes place chiefly through these structures, much as in the Zygoptera of the Odonata.

Welch (1922) has studied the respiratory mechanisms in aquatic Lepidoptera larvae of the genera *Nymphula* and *Cataclysta*. In both of these genera there are species with gills and species without them and no known intergrades. In both the gilled and non-gilled forms the tracheal system is of the holopneustic type, that is, the spiracles and connecting tracheae are morphologically open. In the non-gilled types, respiration is either carried on between the blood and the water through the body wall or else the larva ascends to the surface and opens its spiracles. In the gilled types there are gills of two different kinds—tracheal blood gills, the more complex, in which there are both tracheae and blood, and blood gills in which blood only is found. The tracheation of the body is practically unmodified from that of terrestrial forms.

The air stores carried beneath the surface of the water by some of the large diving beetles and bugs probably have a hydrostatic as well as a respiratory function, and serve to bring the animal to the surface whenever the swimming movements are stopped or the hold on vegetation is released. Brocher (1909, 1911, 1912) demonstrated such a hydrostatic function for the air stores of the Corixidae, Dytiscidae, Hydrophilidae, and Notonectidae. He considered that the air stores have no respiratory function, since he could not demonstrate that the animals made respiratory movements while submerged. However, Babak (1912) and van der Hyde (1922) have shown that respiratory movements do occur in *Dytiscus* while beneath the surface, and Ege (1918) and van der Hyde have shown by gas analysis that the oxygen of the supply is consumed during the stay under water. In studying the mechanism of breathing in *Dytiscus*, van der Hyde observed the movements of a droplet of petroleum when the animal was allowed to breathe in a space closed by this droplet. Inspiratory and expiratory movements, both when the animal was submerged and when it was at the surface, were recorded by the droplet. When the beetle comes to the surface the end of the abdomen pushes through the surface film. The two elytra are then slightly raised and the large space between the back of the abdomen and the elytra is put into free communication with the atmospheric air. Supposedly the air is renewed. The edge of the abdomen is waxy and water does not enter the dorsal space. After the beetle has opened its elytra at the surface there is a short pause, followed by an expiration from the spiracles. Immediately after the expiration the animal usually dives. Analysis of the air store soon after diving showed 0.65 per cent of carbon dioxide, 14.01 per cent of oxygen and 85.34 per cent of nitrogen. After being submerged for some time the analysis showed 0.64 per cent carbon dioxide, 3.05 per cent oxygen and 96.31 per cent nitrogen.

Ege (1918) considers that the air stores have a respiratory function, but not that usually accepted. He believes that the air stores enable the holopneustic animal to utilize the dissolved oxygen of the water. When the oxygen tension in the air store becomes less than that in the surrounding water, oxygen will diffuse into the store, the rate depending upon the tension difference and the area of the free surface for diffusion. The carbon dioxide produced by the animal will diffuse out in the same way, but at a much faster rate than the oxygen diffuses in. The proportion of nitrogen in the store will thus tend to accumulate and will acquire a partial pressure greater than the tension of nitrogen in the surrounding water. The nitrogen will then diffuse out, the volume of the store will be decreased, and no more oxygen can be obtained from the water. Ege considers that the beetle comes to the surface chiefly to renew the supply of nitrogen.

It seems probable that Ege's idea of the action of the air store, while correct theoretically, is not important practically. The small area offered for diffusion, and hence the slow rates of passage of oxygen and nitrogen into and from the store, make it likely that the oxygen is used up long before there is a marked decrease in the volume of the store. Van der Hyde has calculated the quantity of oxygen which could diffuse into the store to be about 0.52 cubic millimeter per minute. According to Ege's figures, one *Dytiscus* consumes in one minute about 8 cubic millimeters of oxygen. The discrepancy between the amount the animal uses and the amount which could be supplied by the water is evident.

Van der Hyde further studied the relative importance of the gases in the water and in the air for the animal's behavior by varying the gas content of the water and the composition of the atmosphere. If boiled water is used, the animal goes to the surface more often, presumably because the air in the air store diffuses out and dissolves in the water. But if boiled water was cooled and then saturated with carbon dioxide, the beetle went to the surface less often. In an atmosphere of carbon dioxide above water containing oxygen, the beetle remained at the surface.

In concluding this review it must be repeated that no complete or detailed summary of our knowledge of the process of respiration in insects has been attempted. The large fields of metabolism and the effects of temperature on the respiratory exchange have been touched only casually for illustrative purposes. The attempt has rather been to present some of the fundamental lines of inquiry into the general subject, and to illustrate these with pertinent references to both the older and the more recent literature. The viewpoint has been constantly in mind that the remarkable success of the insects as a group has been conditioned by the development of efficient respiratory mechanisms, adequate for supplying oxygen for the considerable energy releases necessary in active movements and in flight, and adapted for use under the most varied habitat conditions.

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THE PALAEOMORPHOLOGY OF THE HUMAN HEAD: TEN STRUCTURAL STAGES FROM FISH TO MAN

PART II. THE SKULL IN NORMA BASALIS

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INTRODUCTION

IF WE make careful comparisons of the skulls of recent fishes, amphibians, reptiles, birds and mammals, including man, we can hardly fail to recognize either the existence of class types of skull patterns or the gradually changing ground-plan that underlies the entire series; and if we study the separate bones that together make up each of these skulls we readily identify some of the homologous elements throughout the series, while as to other elements the differences among recent forms of different classes may be so great as to leave some uncertainties which even the most intensive purely morphological analysis may fail to clear up. When, however, we extend our comparisons to include both fossil and recent vertebrates of all known orders, experience shows not only that the patterns of the skulls, especially in the side view, afford one of the most reliable sources of evidence as to the relationships of the forms that bore them, but also that the great differences observed between recent forms of the different classes are more or less completely bridged by intermediate conditions which in the end may leave little doubt as to the origin and evolution of such troublesome elements of the mammalian skull as the vomer, the presphenoid, and the great wing of the evolution of the human skull as here summarized is based upon many general results of modern systematic zoology, palæontology, phylogeny and morphology.

Hence the selection of specimens to illustrate the evolution of the skull from fish to man is not the result of arbitrary choice or preconceived theory on the part of the author. It is the result first, of the labors of all those who have determined the systematic position and phylogenetic relationships not only of the forms that were finally admitted to the series but also of all other forms that might be considered to have claims to stand in or near the line of ascent from fish to man; secondly, each of the series finally adopted for the present purpose was a residuum after the elimination of all other forms which were more specialized than it was, away from the main line of ascent and toward terminal vertebrate forms other than man. Finally, a skull was admitted to the series if its pattern as a whole and in its component parts exhibited one series of characters that plainly foreshadowed the later forms and another that was inherited from earlier stages.

The resulting series doubtless does not constitute a direct phylogenetic series from fish to man, which in practice must ever remain an unattainable ideal, but it no doubt as to the evolutionary history as a whole and as to the main changes of the principal skull elements.

In the present article the history of the norma basalis of the skull is considered. Owing to the great rarity and imperfect preservation of fossil skulls of many of the stages figured in Part I (QUART. REV. BIOL., Vol. II, pp. 267–279. 1927), it is not practicable to show the basal aspects of all the forms used in the side view series. More or less nearly related forms have therefore been substituted, under the condition that their norma basalis is substantially similar to that of the form figured in the series of side views, at least in respect to its supergeneric group characters.

In a general way the elements visible in the norma basalis of the premammalian vertebrate skull may be classified as follows:

I. Jaw elements.
  A. Outer or secondary jaw: comprising dermal elements, the premaxillæ (*pmx*), maxillæ (*mx*), jugals (*ju*) and quadratojugals (*qj*). The jugal also belongs in the circumorbital series and thus has a double function. The quadratojugal is also classified as one of the temporo-mandibular series in the side view.
  B. Inner or primary jaw: comprising
    1. The pterygoquadrate arch, preformed in cartilage; including the epipterygoids (*ep*), pterygoids (*pt*) and quadrates (*qu*).
    2. The adherent tooth-bearing dermal elements: prevomers (*pv*), palatines (*pl*), pterygoids (*pt*) and ectopterygoids (*ectpt*).

II. Keel bone (parasphenoid, *pas*); originally forming the median dermal base of the cranium, underlying the ethmoid and basisphenoid.
III. Basicranial elements:
  A. Basisphenoid (*bs*), including basipterygoid processes for articulation with the pterygoids.
  B. Basioccipital (*bo*), exoccipital (*eo*).
IV. Temporal element: squamosal (*sq*).
V. Otocranial elements:
  A. Proötic (*pro*);
  B. Opisthotic (paroccipital, *opo*).
VI. Hyobranchial elements:
  A. Stapes (*stp*).

The various openings or fossæ seen in the norma basalis of the vertebrate skull are of great importance as landmarks. They include the following:

(1) Paired internal nares (*nar*);

(2) Interpterygoid fossa, lying between the opposite pterygoids;

(3) Temporo-mandibular fossæ, lying between the jugals and quadratojugals on the outer side, the quadrates behind, the pterygoids medially and the ectopterygoids anteriorly. These openings give passage to the jaw muscles as they pass downward from the temporal fossa to the mandible. They may be traced securely from fish to man.

REVIEW OF THE TEN STRUCTURAL STAGES IN NORMA BASALIS

Stage I. Devonian lobe-finned ganoid, Eusthenopteron

Figure from Watson, mostly after W. L. Bryant.

The stages leading up to this form are not known, except in so far as the ostracoderms and the sharks illustrate two successive stages in the evolution of the jaws. In the other direction this fish

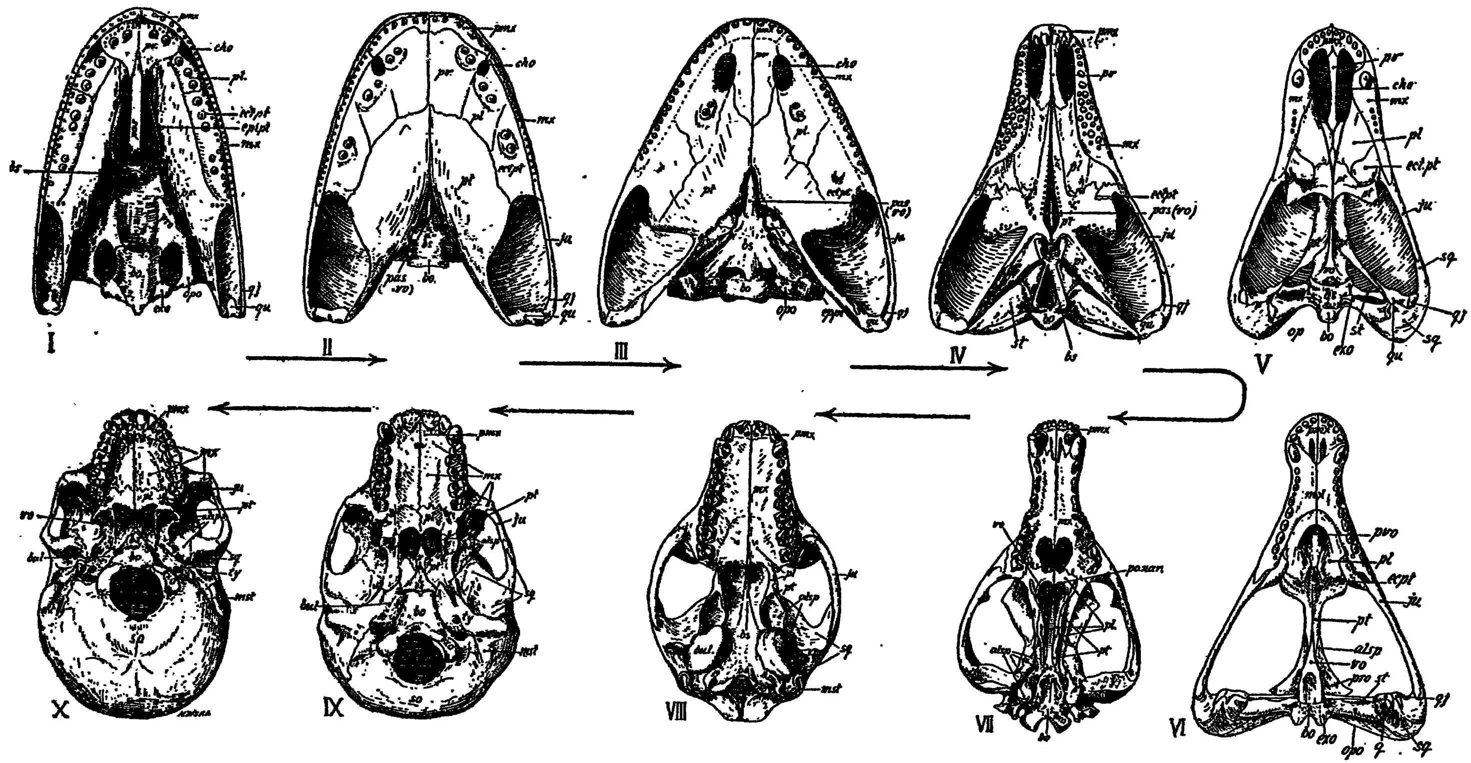

Fig. 1. Evolution of the Skull in Norma Basalis

Stage I. Devonian lobe-finned ganoid, *Eusthenopteron*. Figure from Watson, mostly after W. L. Bryant.
Stage II. Lower Carboniferous embolomerous amphibian, *Eobaphetes*. Figured by Watson.
Stage III. Primitive Permo-Carboniferous reptile, *Seymouria*. Figure from Watson; data from Broili, Williston, Watson.
Stage IV. *Captorhinus*, advanced cotylosaurian reptile of the Permian. Figure and data from specimen. Data also from Broom, von Huene, Sushkin.
Stage V. *Scylacops*, primitive mammal-like reptile of the Middle Permian. Figure and data from Broom.
Stage VI. *Cynidiognathus*, advanced mammal-like reptile of the Triassic. Figure from Broom. Data from Seeley, Haughton, Broom.
Stage VII. *Thylacinus*, modern marsupial mammal, representing a survivor of Cretaceous marsupial stock. Figure and data from specimens.
Stage VIII. *Adapis*, representing Eocene lemuroid primates. Figure and data from Stehlin.
Stage IX. Chimpanzee, representing a little-modified survivor of the Miocene anthropoid stock. Figure and data from specimen.
Stage X. *Homo sapiens*, represented by aboriginal Australian, survivor of Pleistocene man.

already foreshadows man in the groundplan of its skull and is indeed far nearer to him in essentials than it is to its protochordate starting-point.

The general form of this skull has been determined by many conditions and factors, including the following:

(1) the predaceous habits of this long-jawed, snapping fish;

(2) the general flattening of the head and throat, possibly associated with the habit of lying on the muddy bottom.

The articular surfaces for the lower jaw are located far back, immediately behind the plane of the occipital condyle, this arrangement permitting a very wide gap and enabling the fish to seize its living prey in a position favorable for killing and swallowing it. The posterior position of the quadrate may also be associated with the possible ability to tilt the forepart of the head upward after the fashion of a crocodilian, as suggested by Watson.

In conformity with the length of the jaws, all the elements of the outer and inner jaws have plenty of room, that is, none of them are squeezed or crowded out of existence. The ectopterygoid (as determined by Watson) is remarkably long.

The dentition is of the snapping type, requiring only vertical movements of the mandible. The parallel rows of teeth in the lower jaw alternate and fit between corresponding rows in the upper, the larger, more medial rows of teeth being in the most favorable position for piercing and killing the prey held in the roof of the mouth. The prevomers also are remarkably large and, if classified according to function, belong with the dermal plates covering the primary upper jaw. The pterygoids forming the sides of the roof of the mouth are steeply arched to allow room for the prey as it is held while being killed by the snap of the lower teeth.

The huge primary jaws are attached chiefly to the dermal skull roof, laterally by sutural contacts with the quadratojugals, maxillæ, premaxillæ; vertically, through the broad epipterygoids to the skull roof. Ventro-laterally they are braced against the basisphenoid through the basipterygoid processes. As a whole the arrangements recall the conditions in the amphistylic sharks and we may thus think of the crossopt as a shark with a bony mask over its whole head. The jaws need but little bracing against the skull, because the primary upper and lower jaws are squeezed by the adductor mandibulæ muscles against each other rather than against the skull. The quadrate is tied into place and prevented from slipping backward by the quadrate flange of the pterygoid and the sheet-like quadratojugal. It is thus evident that the greater part of the muscular force is expended dorso-ventrally against the pterygoid and only a small part of it would tend to displace the jaw with reference to the brain trough.

The skull appears structurally weak on the lower side because the keel bone (parasphenoid), which ordinarily in fishes extends from the ethmoid region back to the basioccipital, is here limited to the front part of the skull. Nevertheless the chief function of the parasphenoid is not to brace the jaws but to protect the brain trough. Also the small basisphenoid is evidently sufficiently strong to take up the lateral thrusts resulting from uneven application of muscular power.

Behind the parasphenoid is a large vacuity. We do not know whether this vacuity gave passage to an open hypophysio-pituitary tract or whether its presence enabled the fish to raise the forepart of its head upon the back part (as suggested by Watson).

That *Eusthenopteron* was an air-breathing fish and therefore possessed a lung, like that of the related dipnoans, is rendered probable by the presence (according to Bryant and Watson) of internal narial openings lying between the premaxillæ, maxillæ and palatines.

In the occipital region of *Eusthenopteron* we note a wide expansion and forward extension of the otic capsules containing the semicircular canals on either side of the occipital segment. The basioccipital is well developed and forms the thrust block between the vertebral column and the skull. The exoccipitals are figured as distinct from the opisthotic.

Stage II. Lower Carboniferous embolomerous amphibian, Eobaphetes

Figured by Watson.

In this remarkably primitive amphibian we are impressed by the retention of a fundamentally piscine palate, all the elements of which are directly comparable with that of *Eusthenopteron.*

(1) There is a complete development of both primary and secondary jaws, with all components present, at least as seen from the basal aspect.

(2) The arrangement of the dentition is essentially crossopterygian, with a row of small teeth on the outer jaws and a series of large labyrinthodont tusks on the dermal covering bones of the inner, or primary jaw.

(3) The internal nares open inward, behind the premaxillæ and between the prevomers and the palatine.

(4) There is a restricted movement of the head upon the column, indicated by the truncate basioccipital articular surface.

On the other hand, this primitive amphibian already foreshadows the later tetrapods in the ground-plan of the norma basalis. There is a marked contrast in the position of the parasphenoid, which together with the lateral basipterygoid processes, is now displaced backward nearly to the occiput. We do not fully understand the reasons for this contrast; possibly, as suggested by Watson, the amphibian may be derived from fish other than the rhipidistians, in which the parasphenoid extended backward to the occipital region. Or the basisphenoid may have been pushed backward, due to a possible rearrangement in the position of the eyes consequent upon the change from water-living to amphibious habits. In the amphibians as a rule the eyes lie much farther back than in either the rhipidistians or the dipnoans. Also the olfactory chamber is larger. For these reasons the floor of the orbits in the amphibians, in so far as it is formed by the palatine and ectopterygoid, together with the floor of the olfactory chamber (the prevomer) is displaced far backward and inward. A third and perhaps the most probable assumption is that, in addition to the backward displacement of the eyes and the enlargement of the olfactory chamber, there was also a marked decrease in the size of the semicircular canals, which in many primitive fishes are much larger than those of amphibians. The latter change would result in the occipital region's being displaced forward until it came to lie immediately behind the basipterygoid processes.

In conformity with the foregoing displacements the temporomandibular fossæ are now opened up, the pterygoids are beginning to be modeled in the direction of those of more typical tetrapods and the interpterygoid space is greatly restricted.

Stage III. Primitive Permo-Carboniferous reptile, Seymouria

Figure from Watson. Data from Broili, Williston, Watson, Romer.

This form is so primitive (for a reptile) that Sushkin and Broom prefer to remove it altogether from the Class Reptilia. It was indeed a survivor of the earlier amphibians in the following features:

(1) In the arrangement of all the elements of the primary and secondary upper jaws;

(2) In the presence of separate ossicles (the "mesopterygoids" of Broom), lying between the basipterygoid processes of the basisphenoid and the pterygoids;

(3) In all the relations of the stapes, which, unlike that of reptiles, does not articulate with the quadrate (Sushkin);

(4) In the labyrinthodont character of the teeth (Broili);

(5) In the truncate form of the circular occipital condyle, which is broadly pierced by the notochord.

On the other hand, the whole norma basalis appears to afford a favorable starting-point for those of the higher tetrapods and both Watson and Romer argue that the amphibian connection of the stapes is not irreconcilable with primitive reptilian affiliations. The modelling of the pterygoids has proceeded in the direction of the reptiles and there is already a tendency for the anterior process to be narrow and for the descending processes to be developed.

Stage IV. Captorhinus, advanced cotylosaurian reptile of the Permian

Figure and data from specimen. Data also from Broom, von Huene, Sushkin.

Inspection of the figure will show that this form has retained many fundamental characters of its predecessors. On the other hand, the norma basalis has almost reached the stage formerly called the "rhynchocephalian palate," in recognition of the relatively primitive character of the palate of the existing *Sphenodon*. Probably the small size of the parasphenoid may carry this a little out of the direct line of ascent and toward the more typical reptiles, but on the whole it presents a very generalized reptilian stage structurally ancestral to that of the mammal-like reptiles. Thus, the pterygoids are already pinched in toward the midline; the occipital condyle is ball-like and the stapes is in contact laterally with the quadrate. The form of the forepart of the skull as a whole distinctly approaches that of the theromorph series.

Stage V. Scylacops, primitive mammal-like reptile of the Middle Permian

Figure and data from Broom.

At a superficial glance the norma basalis of this skull retains much that is characteristically reptilian; for instance, the anterior position of the internal nares, the strong development of the pterygoids, the unimpaired quadrates and the single ball-like occipital condyle. But a nearer view discloses a series of characters that prophecy the higher grades of this order and the advent of the mammals.

(1) There is a prophecy of the mammalian secondary palate. Dr. R. Broom informs me that on either side of the elongated internal narial opening there is a horizontal ridge on the maxilla and the palatine, which apparently marks the attachment of the fleshy palate, so that in life the inspired air was probably passed backward above this fleshy bridge to the opening in the U-shaped depression of the palatines.

(2) A notable advance toward the mammalian condition is seen in the marked reduction and slenderness of the posterior or quadrate ramus of the pterygoid.

(3) The squamosal has become conspicuous as the main brace of the zygomatic arch and together with the jugal is substantially in the primitive mammalian position at the posteroexternal corner of the skull.

(4) The opposite pterygoids have been pinched together along the midline, doubtless affording insertion to the strong pterygomandibular muscles.

(5) The keeled parasphenoid in the ventral aspect is beginning to assume the appearance of the mammalian vomer and Dr. Broom informs me that cross-sections of the skull of a typical gorgonopsian demonstrate the complete correspondence and homology of the parasphenoid with the mammalian vomer.

(6) The ectopterygoids are notably reduced in size and are approaching their final disappearance.

(7) The palatines are beginning to draw away from the front part of the skull and to take up their position in the middle of the palate.

(8) The dentition is differentiated into incisors, canines and cheek teeth.

(9) The stapes has precisely the same relations to the quadrate that its homologue in the mammals does with the incus, a point which will be more fully noticed below.

(10) The inner ear is displaced toward the ventral side of the skull.

Stage VI. Cynidiognathus, advanced mammal-like reptile of the Triassic

Figure from Broom. Data from Seeley, Haughton, Broom.

The norma basalis reveals a form that is evidently related to the gorgonopsians (Stage V) but which has advanced far beyond them in the direction of the Mammalia.

(1) The secondary bony palate, consisting of horizontal flanges from the maxillæ and the palatines, is complete and composed of the same elements as in the mammals.

(2) The pterygoids are diminished in importance, especially the quadrate ramus, which has been partly crowded out by

(3) The progressive development of the epipterygoid, which has assumed the characters of its homologue, the mammalian alisphenoid. This element has precisely the same position and nearly the same attachments as the mammalian alisphenoid and its homology with that element is extremely probable (See Gregory and Noble, 1924).

(4) The quadrate is now notably diminished and the quadratojugal slightly more so; so that a further continuation of the same tendency would reduce the quadrate to the size of the mammalian incus, with which there are many reasons to identify it.

(5) The zygomatic portion of the squamosal is substantially mammalian in all its essential relations.

(6) The temporo-mandibular fossæ have nearly assumed the mammalian character.

(7) The occipital condyle has become double and although the median portion is formed of the basioccipital, the exoccipitals contribute to the lateral portion (Broom).

(8) The stapes corresponds to the mammalian stapes in its connection with the inner ear on one side and with the quadrate (= incus) on the other.

(9) The ectopterygoid, as identified by Broom, is reduced.

(10) The dentition has attained the completely mammalian grade of differentiation into incisors, canines, premolars and molars. The adult dentition is preceded by a single set, representing the deciduous incisors, canines and premolars (Broom). Apparently the molars have no deciduous predecessors.

On the other hand, the vomer (parasphenoid) retains much of its primitive posterior position. That this bone is the homologue of the vomer is indicated by the fact that in *Dicynodon* the same element has an anterior process which immediately underlies the presphenoid (Broom).

Stage VII. Thylacinus, modern marsupial mammal, representing a survivor of Cretaceous marsupial stock

Figure and data from specimens.

This modern form represents very well the essential architecture of the skull that was apparently characteristic of the Cretaceous polyprotodont marsupials. It is not in the direct line of ascent but is nevertheless typical on the whole of the primitive mammalian stage. The dentition of *Thylacinus* is of a relatively primitive mammalian type, the general pattern of the premolars and molars being inherited in basic features from the primitive placental mammals of the Cretaceous period.

Great advances beyond the cynodont stage are seen in the following characters:

(1) The completion of the mammalian secondary palate by the backward production of the palatine bar behind the level of the cheek teeth.

(2) The complete disappearance of the quadrate from the norma basalis and its retreat into the cavity of the middle ear.

(3) The completion of the modelling of the zygomatic portion of the squamosal for the support of the mandible, correlated with the development of a new or distinctly mammalian contact between the ascending ramus of the dentary and the glenoid region of the squamosal.

(4) The loss of the postorbital element, including the bar connecting the frontal and the jugal.

(5) Great diminution of the pterygoids, which are functionally replaced by the pterygoid flanges of the now dominant alisphenoids.

(6) Forward retreat of the vomer from the basisphenoid, exposing the latter in the ventral view.

(7) Development of a middle ear chamber or cavum tympani, in this case covered by a bony shell from the dominant alisphenoid.

(8) Withdrawal of the true otic elements from the plane of the base of the cranium; in this case they are largely covered by the alisphenoid bullæ.

(9) Completion of the paired occipital condyles.

Stage VIII. Adapis, representing Eocene lemuroid primates

Figure and data from Stehlin.

A great advance beyond the primitive mammalian condition is recorded in the norma basalis of this relatively early primate. Three leading factors have conditioned this advance, as follows:

(1) The elaboration of the upper molar teeth from the primitive tritubercular carnivorous to the quadritubercular frugivorous stage with incipient changes in the same direction in the posterior premolars. The incisors, now reduced in number to two on each side, have acquired more or less chisel-shaped crowns. The form of the canine is better adapted for frugivorous than carnivorous habits.

(2) The peculiar development of the dentition described above doubtless has conditioned the broadening of the jaw muscles and of the secondary palate, together with the shortening and broadening of the pterygoid region; the fossæ for the origin of the pterygoid muscles being conspicuously developed.

(3) The anteroposterior shortening of the jaws, correlated with the change from snapping and shearing to piercing and cutting, has caused the glenoid fossa to be displaced forward considerably in front of the basioccipital.

(4) A marked increase in the volume of the brain has conditioned the widening of the basicranial region.

(5) The chamber of the middle ear has become greatly enlarged and covered by the entotympanic, a bone of disputed origin but probably a neomorph derived from the extension of bony tissue around the inner side of the tubotympanal expansion. The true tympanic bone lies within this cavity covered by the entotympanic.

(6) Another indication of advance beyond the primitive mammalian stage is the beginning of the downward flexure of the basicranial axis upon the axis of the vertebral column, indicated by the partial exposure of the foramen magnum in the ventral aspect.

Stage IX. Chimpanzee, representing a little-modified survivor of the Miocene anthropoid stock

Figure and data from specimen.

A great advance in the direction of man has been achieved by this animal, which is indeed far nearer to man than it is to the primitive lemuroid of Stage VIII. The dominant factors in this advance have been the great increase in the volume of the brain, the marked downward flexure of the skull upon the column correlated with more or less erect position during locomotion in the trees. Again, in response to advanced frugivorous adaptations, the jaws and palate have been much shortened anteroposteriorly. The dental formula is reduced to that of man. The premaxillæ are fused with the maxillæ. The central chisel-like incisors are widened, perhaps for the cutting of fruit and tender shoots. The palatines have now completed their retreat to the posterior end of the palate. The pterygoids have shrunken into slender delicate slips of bone which are closely appressed to the descending flanges of the sphenoid. The retreat of the vomer toward the palate is also complete. The true tympanic bone has now escaped from its confinement within the cavity of the entotympanic and has fused with the expanded periotic, which forms the remnant of the ancient bulla.

The foramen magnum is widely exposed in the norma basalis and the mastoid portion of the periotic is expanded.

The temporo-mandibular fossæ are much shortened anteroposteriorly in correlation with the forward displacement of the squamosal and its glenoid cavity. The anterior part of the zygomatic arch forms a sharp elbow with the projecting process of the maxilla.

Stage X. Homo sapiens, represented by aboriginal Australian, survivor of Pleistocene man

Figure and data from specimen.

No more convincing evidence of man's derivation from a primitive anthropoid stock could be afforded than the fundamental resemblance of this skull in the norma basalis to that of the chimpanzee. At nearly all points it has advanced beyond the chimpanzee in the same direction in which the latter had progressed beyond the primitive Eocene primate. Thus there is a further shortening of the jaws, a further constriction of the temporo-mandibular fossæ, a further angulation of the maxillary with the jugal, a further forward displacement of the squamosal, a further backward expansion of the braincase, a further exposure of the foramen magnum, due to the more pronounced cranial flexure, and so forth.

Special human features are seen in the shrinking of the canine teeth and of the forepart of the palate, in the marked diminution of the bulla and its conjoined tympanic bone, also in the downward growth of the mastoid process.

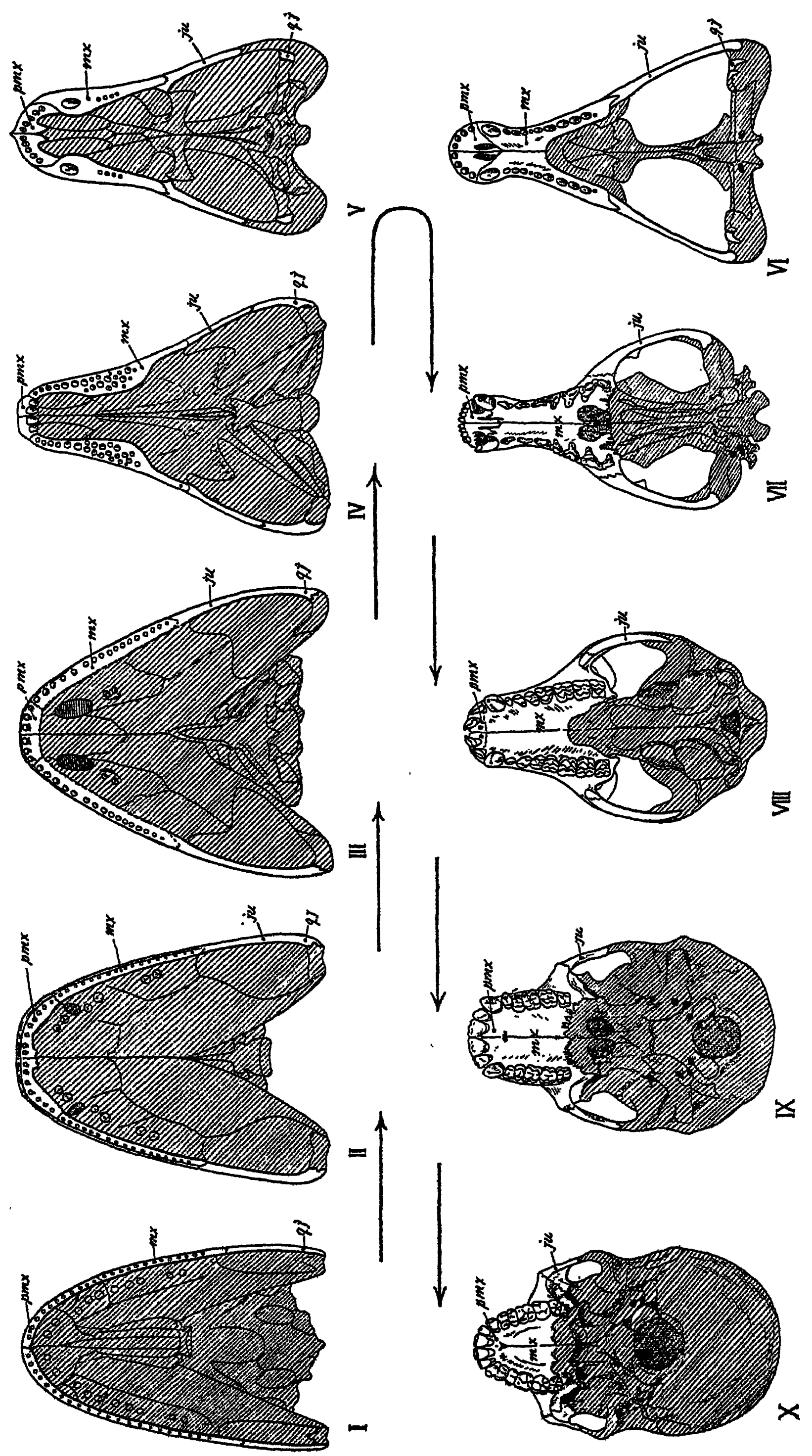

FIG. 2. EVOLUTION OF THE OUTER JAW SERIES

Same stages as in Fig. 1. White = *pmx, mx, ju, quj*. Cross-hatched = all the rest.

HISTORY OF THE INDIVIDUAL ELEMENTS OF THE SKULL

I. Jaw elements

A. Outer, or secondary jaw. In Stage I the dermal plates are far less differentiated from each other than in the final stage. Thus the premaxilla and the maxilla in norma basalis form narrow strips bearing small similar teeth forming part of the general bony mask of the face. The jugal and quadratojugal are in series with these elements. By the time we have reached Stage V, marked differentiation in this series has become apparent. In Stage VI the quadratojugal is reduced almost to vestigial proportions and the jugal has almost acquired its mammalian character. The premaxillæ and maxillæ both have secondary palatal plates. With the loss of the quadratojugal in the early mammals, together with the loss of the postorbital bar, the conditions advanced toward the human stage. In Stage IX, represented by the chimpanzee, the premaxilla is fused with the maxilla in the adult, just as in man. The jugal is now limited to the front part of the zygomatic arch. In the final stage the contrast between the surviving elements of the secondary jaw series reaches its climax. The quadratojugal maintains its place in series with the secondary upper jaw and as an outer brace of the primary upper jaw throughout the first four stages, but becomes greatly reduced in Stages V and VI and disappears in mammals.

B. Inner, or primary jaws. The outstanding features of the history of this series of elements are:

(1) Steady diminution of the prevomers, which finally disappear from view early in the mammalian grade.

(2) Backward and inward displacement of the palatines, which are widely separated originally but finally meet in the midline (Stage V) and are found at the back part of the palate in Stages VI to X.

(3) Progressive reduction of the ectopterygoids, which are reduced almost to a vestigial condition in Stage VI and are absent in later stages.

(4) Modelling and extreme reduction of the pterygoids. In Stage I these are the dominant element of the primary upper jaw, widely separated in the midline. By Stage IV they have become highly differentiated, having no less than four main processes, not the least of which is the quadrate branch of the pterygoid. By Stage V this process begins to weaken. In Stage VI its place is largely usurped by the growing epipterygoid (alisphenoid). In mammals, Stages VII to X, the pterygoids are reduced to slips on the inner side of the descending flanges of the alisphenoid, where they are found in man.

(5) The quadrate maintains its primitive condition through the first four stages of the series, but in Stages V and VI its function as a supporting element is partly usurped by the progression of the zygomatic branch of the squamosal. In Stage VI the quadrate is a small element which however still retains its function as the suspensorium of the mandible. By Stage VII the quadrate has disappeared from view, being transformed into the minute incus of the middle ear.

II. Keel bone

The vomer or parasphenoid always has a double relationship: on the one hand with the median septum of the nasal chamber and on the other hand with the roof of the mouth and the basisphenoid. In the mammals, including man, the vomer has lost its posterior extension over the basisphenoid and is found as a small element dividing the naso-pharyngeal tunnel in the midline.

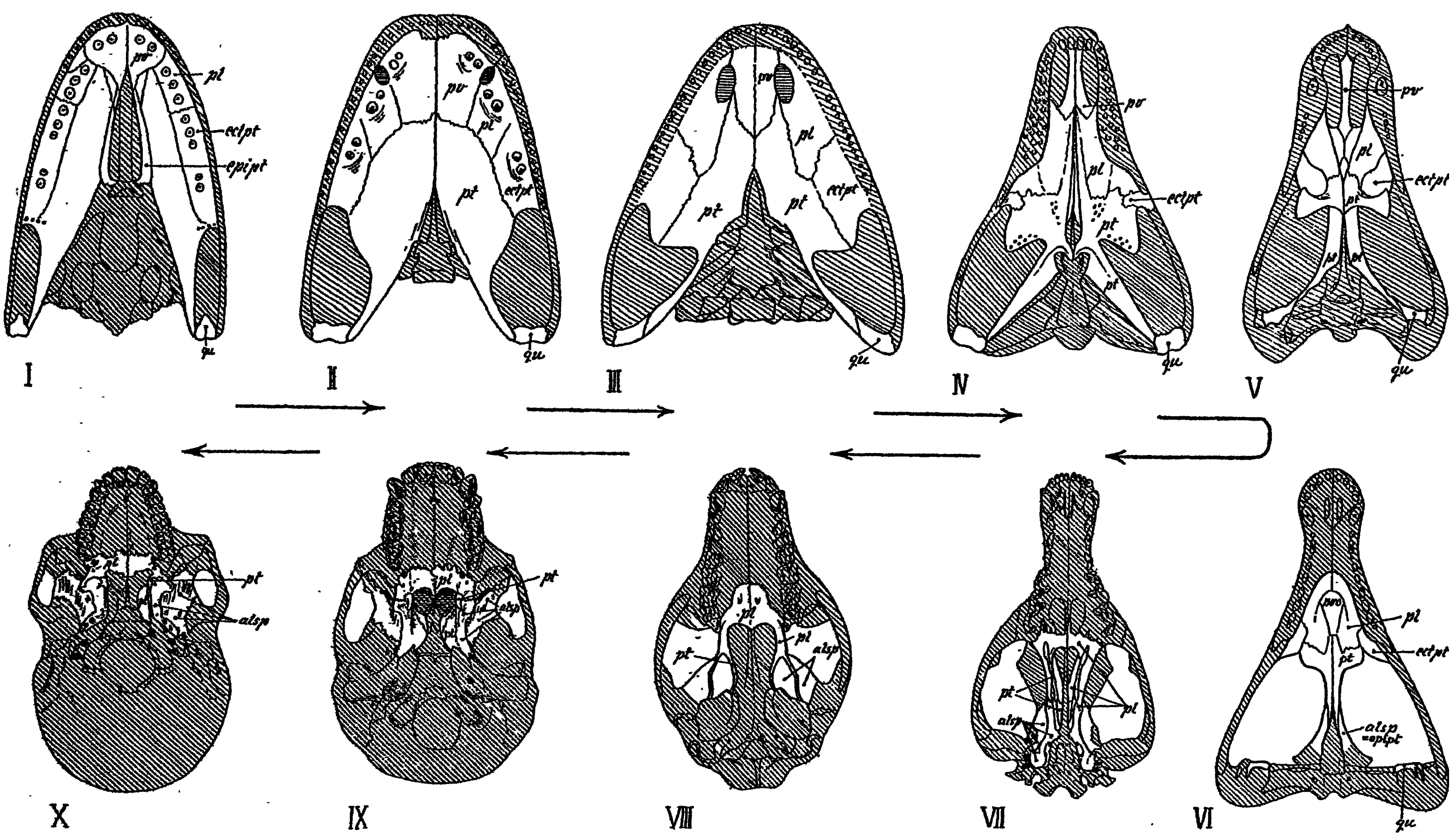

FIG. 3. EVOLUTION OF THE INNER JAW SERIES
Same stages as in Fig. 1. White = *pv*, *pl*, *ectpt*, *pt*, *epipt*. Cross-hatched = all the rest.

III. *Basicranial elements*

The basisphenoid underlying the pituitary region of the brain in the early amphibians is covered by the parasphenoid but with the retreat of this element it is revealed as the central piece of the base of the cranium. In the early amphibians the basisphenoid sends out strong basipterygoid processes, which are covered by corresponding processes from the pterygoids. With the reduction of the pterygoids these processes lose their importance and disappear as we approach the mammals.

The basioccipital always constitutes the thrust-block between the vertebral column and the skull. In the lower vertebrates there is little movement between it and the column, but by Stage IV it has acquired a ball-like condyle which becomes subdivided into paired occipital condyles in Stage VI. These are at first located chiefly on the basioccipital but in the succeeding stages they shift apart laterally on to the exoccipitals.

IV. *Temporal element*

The squamosal, a prominent element in the lateral view of the skull, does not appear in the norma basalis until Stage V, where it is beginning to constitute a new suspensorium of the mandible. This immensely important transformation is completed in the cynodonts and in the early mammals. With the great development of the braincase and the flexure of the skull upon the column, the glenoid portion of the squamosal is displaced relatively far forward in man.

V. *Otocranial elements*

The otocranial region is largely developed in the norma basalis of Stage I. In the early tetrapod it forms the side walls of the braincase. By Stage V it has become partly displaced to the ventral side of the occipital region, where it is found in later stages. The sides of the brain trough are concealed from the basal view in all the earlier stages but in the primitive mammal skull, owing to the expansion of the neopallium, they begin to appear in the ventral view; in the chimpanzee and still more in man they become enormously developed.

VI. *Hyobranchial elements*

The history of the middle ear bones from fish to man may be epitomized from the researches of Reichert, Gaupp and many other authorities, as follows: The stapes, or columella, of higher vertebrates is apparently represented in the fish by one of the hyoidean elements, either the hyomandibular, according to most authors, or the pharyngo-hyal, according to Woskoboinikoff, Schmalhausen and Sushkin. In the typical fishes the upper hyoidean segments serve for the support of the operculum of the gill chamber and of the hyoidean gill-arch. With the loss of the gills and operculum, the hyomandibula (or perhaps the pharyngohyal) is retained in contact with the tympanic membrane (which covers the "otic notch" in the position of the now obsolete bony operculum) and transmits to the inner ear the vibrations caused by sound waves impinging against the tympanum. In the mammal-like reptiles the outer end of the stapes was in contact with the quadrate or posterior element of the primary upper jaw, while the tympanic membrane was probably attached to the squamosal and to the back part of the articular bone of the lower jaw. Thus, as in recent reptiles, the back part of the jaw elements were probably already sharing in the vibrations of the tensely stretched drum membrane. By the time of the cynodonts the quadrate was a small element and the dentary was the dominant part of the lower jaw; the stapes, at least in the smaller cynodonts, was perforated, presumably by the stapedial artery, exactly like the stapes of mammals. When the dentary grew upward and backward and established the new or mammalian joint between itself and the squamosal bone (see Part I of this article) the quadrate and articular bones were relieved of their functions as jaw elements while retaining and intensifying their functions in transmitting pulsations to the stapes and thence to the cochlea of the inner ear. Thus the curious auditory ossicles of man have been derived by change of function from the primary jaw elements and hyoidean arch of the fish. In this connection it is of interest to note that, according to Doran, the auditory ossicles of the gorilla and the chimpanzee closely resemble those of man. The ossicles in mammals become enclosed in a chamber which is a diverticulum of the tubotympanal canal and this in turn is encased in a bony shell, the auditory bulla.

CONCLUSION

A survey of the series as a whole indicates that the bony tracts of the skull often appear to be moulded around or with reference to other structures which are frequently represented by fossæ in the dried skeleton. Thus the shape of the pterygoids is determined partly by their position between the temporo-mandibular muscles on the outer side and the pharynx on the inner side. Even in mammals, in which the pterygoids are greatly reduced, their shape is partly determined by their position in the bony wall of the pharynx. It is also evident that the form of a particular bone is partly determined by its position with reference to the midline of the skull as well as to the axis and direction of locomotion and the resulting orientation of the dorsal and ventral surfaces. Again, the shape of a bone is obviously in adjustment to the particular nature of the stresses (due to gravitation and muscular contraction) to which it is subjected, while on the other hand, its shape limits the movements and conditions the form of parts that impinge upon it, as in the basioccipital condyle. The presence or absence of a given bone in a particular type of skull, its general position and contacts are also obviously determined in part by its phylogenetic history in the stages preceding the present life habits. The increase or decrease of any given bone naturally tends to change the form of the skull as a whole. On the other hand, there appears to be some regulating mechanism, analogous with surface tension, which keeps the members of a functional series more or less in line, more so in the earlier and less differentiated stages than in the later ones. Compare, for example, the subordination of the premaxillæ, maxillæ and jugals to each other and to the parabolic contours of the jaws as a whole in Stages I, II, III, with the bold individuality of each of these elements in Stage VII; also with the later de-differentiation of the premaxillæ and maxillæ in Stages VIII, IX, X.

Whatever may be the complex causes, it is a fact that during a long geologic period a given element such as the ectopterygoid may gradually be relieved of its functions, or in other words, may be crowded out by a more aggressive neighbor. Thus we have the allied phenomena called the "change of function" and the "substitution of one part for the other."

While bones may be pushed apart, grooved or moulded, yet they naturally show a certain conservatism or inertia; otherwise the skull patterns would be so evanescent that we could never homologize elements through long reaches of geological time. The persistence of the skull elements is illustrated by the retention of so many of them throughout the series from fish to man. In the norma basalis this is more marked than in the norma lateralis. Of the full complement of bones present in the fish represented in Stage I, the only ones not preserved in man are the prevomers, ectopterygoids, quadratojugals. Of the rest, the quadrate has been taken over into the middle ear and is hidden from view, the epipterygoid has probably become the great wing of the sphenoid, the parasphenoid has become the vomer, the proötic has probably fused with the opisthotic. All the rest are present although greatly changed in form.

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POPULATIONS OF ANT MOUNDS

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THE social insects, ants, bees, termites, resemble man not only in the numbers living together but in the construction of dwellings so very much larger than the individuals that make them. The number of individuals employed in such constructions is one element of success; yet the number is small in man as compared with these social insects. We can easily count the men who construct or who dwell in either a communal house of the South Sea Islanders or a modern hotel or apartment house, but in the bee hive only laborious methods reveal the fact that the individuals are from ten thousand to seventy thousand in one dwelling, while in a certain dwelling of a termite in Jamaica we counted no less than 631,878 individuals. Of this population about nine-tenths were full grown workers.

Ants in an ant hill have for the most part escaped all exact census and it is our purpose to add something to the scanty knowledge of this aspect of these social animals. The common small ant hills may be but ephemeral byproducts of mining operations, but the large ant mounds constructed of earth both in Europe and in the United States may persist through many years as community houses for successive generations of family groups that build and inhabit them as homes.

In 1906, when K. Escherich wrote his book on the life of ants, he could only report that the most populous ant mounds were those of *Formica rufa*, *F. exsecta*, *F. pratensis*, and *F. exsectoides;* and that in Switzerland the leading student of ants, Forel, had estimated the numbers in a mound of *F. pratensis* to contain 100,000 ants, while Sir John Lubbock, first Lord Avebury, thought 400,000 to 500,000 to be a probable number but that Young had counted from 50,000 to 100,000 in *F. rufa*. That left it in doubt whether the populations of ant mounds are of the magnitude of the termite or the honey-bee populations; and this seems the present-day state of the question.

No data as to numbers are reported for American ants that make large mounds, though the pioneer in the study of these mounds where present in large numbers in Pennsylvania, the Rev. H. C. McCook, was so impressed by the great size of the mounds in comparison with the smallness of the builders that he calculated that man built the great pyramid sixty-nine million times his own bulk, but that the ant built its pyramid-like dwelling six thousand eight hundred million times the ant's bulk.

Here in Maryland this same ant, *Formica exsectoides* F., presents fine groups of mounds not only here and there in the mountains of Garrett County, and in the Blue Ridge, but also near Baltimore, in Baltimore County; and especially over a large area in Montgomery and in Prince George's counties, toward Washington, as made known by the State Entomologist, Dr. E. N. Cory.

HOW CAN WE ESTIMATE THE POPULATION OF AN ANT MOUND?

When first observing these very active insects swarming over the mound and over the food trees that may be one hundred feet distant from the mound, one's impression may be that the population is vast; however it is to be borne in mind that each ant, running at the rate of some fourteen feet a minute, may appear in many places in quick succession, and careful examination shows that the ants are not uniformly distributed all over the terrain but that they are running chiefly in certain paths that lead to their food trees.

By counting the ants on such paths we gain some notion of the actual population that is busy here. From an average sized mound, in five minutes, we noted eighty-three ants running out from the mound toward the tree that supplied food and as many more ants returning. As some ants marked with paint spent often about half an hour away from the mound, there were likely enough five hundred ants making use of this path at one time; and as most mounds have several paths there may well be a few thousands of ants thus out foraging in the territory outside the mound.

At the same time on the surface of the mound one may often see very many ants busy in the maintenance and growth of the mound; hurrying toward the apex, and more rapidly dashing down to the base after having deposited a stick, leaf, or stone for the building. To estimate the numbers of these ants on the mound we hold over them here and there a square wire frame six inches wide, and count the ants circumscribed for a moment by this quarter of a square foot area. The numbers range from eight to eighty on different mounds and upon different parts of the same mound.

An especially large mound calculated to present sixty-two feet of surface was found to be overrun with about sixty ants to the average square foot, as measured in many places, so that there one might see 3,720 ants working on this exceptionally large edifice, at one time.

That the numbers of ants working on a mound may be great is also suggested by the work accomplished; thus when two quarts of small stones, estimated as 56,135 individual pieces of crystalline limestone fragments, were placed at the base of a certain mound, it was found that in three days the ants had carried many pieces up and had scattered them rather uniformly (as is their wont, with building materials), over the surface of the mound with an average of 1,514 stones per square foot or a total of 19,051 stones. Since each stone is carried by only one ant at a time, and though the distance the stones were carried or dragged was less than two feet, one would suppose large numbers to have been at work. This is especially probable as, often, each stone is not carried all the way in one trip but laid down and later carried onwards by another ant, so that the number of portages was greater than the number of stones. However, each ant works very rapidly and for long times and a few hundred will accomplish an astonishing amount of work; yet in three days it is probable that successive sets of ants were engaged in the above task and this means many ants involved.

Besides the ants on the road and on the mound at times of construction there are many ants within the mound, as evidenced by breaking into it and finding many attending the young and in vigorous defense against attacks; while pieces of shingles placed on the mounds revealed in subsequent days large aggregates of ants collected under the shingles to rest in appreciation of the warmth afforded through the insolation of these artificial roofs.

A more definite approach to a census of the population of the mound comes from the observation that in September some mounds are thickly strewn, as with handfuls of wheat, with the cast-off pupa cases or swaddling clothes of the young, brought out by the ants from the interior and strewn as building materials over the mound surface. Each of these represents a new ant added to the population. Counts of these empty cases by the above wire frame gave an average of 212 per square foot or a total of 13,144 for the very large mound. But two days later rain, wind and the accumulation of other building materials had reduced the visible pupa cases to 7,000. Another mound also showed pupa cases at the rate of 200 to the square foot and had this mound the size of the other there would have been 12,400 ants represented.

Thus in the mound, on the mound, and in the neighborhood of the mound, there are thousands of ants that use the mound as their place of origin, to which they return to care for and feed the young. But as many ants work all night in the warmer season there is no time when all the ants can be taken within the dwelling, hence a complete census is difficult.

ANT MIGRATIONS

On rare occasions most of the ants combine in a common hegira, flowing out over the earth to found a new mound and leaving the old one more or less depopulated. This suggests the possibility of counting the population as it migrates. On one occasion for twelve days in July 1926 the ants of a large mound were thus migrating out to a new mound, all in one path from four feet wide to later two feet wide, dwindling as the days went by. This run of ants out of the old mound lasted the greater part of the day time and at any one minute there were as many as forty ants leaving; yet about as many returned, since the ants run in both directions. However, many of these going out carried each a burden, either a full grown worker or else one of the young ants, while few of those returning carried ants. If we could have counted the numbers of ants carried out in excess of those carried back, we might have calculated the entire number of ants taken to the new mound.

With our very imperfect data it seemed only that some thousands of ants were concerned in this migration. But at the speed of running, one ant might cover the forty-five feet from the old to the new mound and return to be counted again every twenty minutes, so that a few hundred ants might have done the chief portage of the carried ants, had they lost no time. In this case no complete census of the old mound was possible, since not all the ants left it permanently but both mounds continued to flourish as populous communities.

Forel, however, was able to base his estimates of the numbers of ants in an average mound of *F. pratensis*, in Switzerland, upon such a migration, which he watched from its incidence onward at times each day for an equivalent of eight days of good weather. Every day the march began at half after nine and lasted about seven hours, stopping rather sharply with the oncoming of the cool nights in May. The ants remained in the old or in the new mound till the following morning, when those in the old mound started the trek again before any ants had come back from the new mound. Forel saw an average of thirty-four adult worker ants carried bodily away from the old mound each minute and on this basis he calculated the entire numbers thus transported to the new mound as 114,000; but, to allow for sources of error in the data, he supposed the sum to have been from 50,000 to 150,000.

Forel then judged that from this average mound having a population of one hundred thousand ants more or less, it might be inferred that a small mound would contain from five to ten thousand ants but that very large mounds might harbor 400,000 to 500,000 adult ants.

These last suppositions were accepted by Sir John Lubbock, who states (10, page 119) that ant mounds are more populous than bee hives and that in larger communities of *F. pratensis* "it is possible there may be as many as 400,000 to 500,000 ants and in other cases even these large numbers are exceeded."

A possible criticism of all estimates of populations based upon actual migrations is that there is no proof that ants carried to a new mound one day may not return another day and themselves act as porters or even themselves be carried several times, which would lessen the calculated population.

TAKING AN ANT CENSUS

A much surer basis for counting the community seemed to be found in the fact that all the ants of a mound retire into a torpid condition within and under the mound every winter and then should be all obtainable in a concentrated space. With this in mind, a certain average sized mound nineteen inches in height, fifteen feet in circumference, and five feet over the top, in Montgomery County, was dug up February 12, 1928. Some description of this region and of the mound-structure may then elucidate the conditions of census-taking by this method.

With small scattered oak and pine trees the thin layer of dark humus full of matted roots of huckleberry, etc., overlies a sticky, light colored clay full of pebbles. Erupting from the subsoil through the humus the mound had spread laterally as a conical mass of gray earth commingled with bits of vegetable matter and such minute pebbles as the ants had collected.

The firm roof of the mound, one to three centimeters thick, was perforated, near the base only, by entrances into the internal labyrinth of passageways running somewhat parallel to the outer surface, but interconnected in different layers by many radial passageways, the whole forming a dense network branching every 40 mm. or so. The network was more dense near the surface, especially that to the south and from it there extended downward beneath the mound some twenty shafts with various side drifts; shafts being seven by seven and others nine by nine millimeters in diameter. Almost all the short passageways of the labyrinth net were wider than deep; of thirty-three measured, only six had equal diameters and twenty-seven ranged from 19 by 9 to 8 by 6 with average of 12–4 by 9. In all these tunnels the roof was markedly different from the floor; the roof or ceiling was rough and with projections of earth and stone as if roughly bitten out, while the floor was smooth as if much trodden when moist.

To obtain the ants a ditch was dug close to the south edge of the mound down to water at two feet depth; the mound was carefully shovelled out and the ants captured by spooning them out from the vertical tunnels, side drifts and the lower labyrinths, in which the ants were found matted together in dense dark masses with intermingled legs; they occurred in separate tunnels as much as two feet apart and not at all in one common bed.

These ants were in the semitorpid state

in which the similar ant *Formica ulkei* was found by Holmquist; all were capable of slow locomotion at temperatures of five and even three degrees C., 20 to 24 inches down in the earth and showed their main responses, climbing and biting at the glass thermometer or seizing hold of bits of cloth and being thus captured; or in some cases carrying mouthfuls of earth, as if to repair the damage done to the mound.

Though the temperature of the air was 5°C., that within the soil only 3°C., and though the thermometer on the north face of the mound, in the sunshine, registered but 4.5° and within the upper part near the stump only zero with fine crystals of ice in the passageways of the labyrinth; yet in the labyrinth of the south part of the mound there was a temperature of 8°, owing to that storing up of sun heat so carefully investigated by Steiner in the mounds of *F. rufa* and observed in *F. exsectoides* by Andrews. It was here that some few ants first emerged, having not yet retired with the majority to the lower levels beneath the mound. Presumably, as in *F. ulkei*, these upper ants may be those that work on the mound top to the last moment long after the main population had gone into semihibernation below.

Yet the most active ants were by no means as active as in summer, and in bottles they gave off little or no odor of formic acid. With the very high water table, some of the ants seemed to be hibernating below water level, since in digging the deeper tunnels water gushed out carrying ants floating upon it, sluiced out by change in pressure conditions and here again it is possible, as suggested by Holmquist, that the ants may hold air in the tunnels even below water level.

The ants collected in jars and cans, alive or dead, were counted at 5°C. on February 13–17, as 4,802 living and 1,005 dead workers with ten living queens, or perfect females, only one of which was injured.

As three people in several hours had failed to dig out all the mound, some of the earth was replaced and left till May 6, in the hope that the remaining population could be captured with less mortality when not deep down in the gravel and clay, even though more active then.

At this date, the temperatures being 17–19°C., the ants were active on the mounds, food trees, and paths getting food from aphids and certain scale insects on scrub pine trees and apparently drinking from injured unfolding leaves. The ruins of the dug out mound were already worked over by the part of the population not removed in February; about an inch deep of pellets had been assembled over the surface of the mound rising above the old stump and here some two hundred ants were now at work. Only a few ants were discovered passing out from this mound to small oak trees some fifteen feet west and east of the mound, and on these very few ants could be found. Two of these were drinking juice from an injured shoot, with unfolding leaves about two inches in length, and it seemed that this juice arose from injuries in the stem caused by insect larvae. Though a dozen or twenty of these ants were busy struggling to bring home a small millipede on the ground, it did not appear that this population had as yet any well established source of food, even though it had done so much work in reconditioning the mound.

To collect these active ants they were stimulated by drawing bits of rag slowly over the mound and then when the pugnacious ants had seized or mounted upon the rags they were thrown into a large milk can or else the ants were shaken off into it. After removal of all ants on the surface, the mound was dug into and the ants removed in the same way, as they swarmed out of the labyrinths that they had constructed since February. These ants occurred scattered here and there, and some deep down in the wet gravel in one mass of twenty or more were still jammed close together as in winter rest, having apparently never been awakened as yet by the outer temperatures. Though the weather had been very hot the temperature where these ants were hibernating was but 14°C. These ants were sluggish, those above were active but not so much so as in summer. This is in close agreement with the findings of Holmquist that in *F. ulkei* Emory, some ants lingered on in hibernation up to May 14.

All the ants collected in four hours by three people were counted May 9 and 10 with the expedient of lowering a glass rod into the container in which the ants were active and then removing it when a few had responded to this attack by mounting upon and seizing the rod; these five to ten were counted and brushed off with the fingers into a receptacle. The few remaining dead ants were dumped out and counted individually. The living were 2,322 and the one queen and the dead were only 99, making 2,422 to be added to the part of the population collected in February. This made a total ant population of 8,239, of which 11 were queens, and 8,228 workers; 7,135 being counted alive and 1,104 when dead.

Doubtless this census was not entirely complete, since several hundreds may have perished in the wet clay in February and some few may have been out on foraging parties in May, while even this second digging could not have discovered quite all the population. Hence the dug out mound was visited again on November 18, 1928, when on account of the exceptional warmth, with temperatures of 26° in the air and 20° within the mounds, and 33° on the apex in the sunshine, ants were still working on the mounds in that region. Yet the remainder of the dug out mound showed no life, the temperature within it was but 17°; digging revealed no ants. There were, however, evident signs that ants had done considerable work in reconstructing labyrinths in two distinct piles of earth thrown out in former diggings; but the washed condition of the surface, as well as the presence of open holes, showed that the ants had not carried on the usual fall completion of the mound as had other populations, and we inferred that the few ants that had been left from the digging in May had finally disappeared, possibly from old age, and from lack of a queen.

The counts from these three successive visits thus assign to the community when it went into winter quarters in the fall of 1927 a population of 8,239 plus whatever ants escaped counting, from death in the digging or from other causes, or escaped at the time of the May census.

It may be a conservative surmise that the entire population was ten thousand adult ants in this average domicile of *Formica exsectoides*. Thus far there are no data to show that this ant has ever such vast populations as those estimated by Forel and accepted by Lubbock for similar ant mounds in Europe. That these latter estimates were excessive seems evident from the results got by more precise methods in Switzerland by Emile Young, who, in 1897 and 1899, made for the ant *Formica rufa* the most satisfactory determinations of populations as yet available.

YOUNG'S OBSERVATIONS

The mounds he studied were all similar to the ones we studied, having about the same base but steeper slopes and greater height; so that the largest had three times the volume of ours. His first method was to count all the ants to be found in a certain populous mound, 60 cm. high and 114 cm. in width, after killing them in a half hour's exposure to carbon disulphide poured into the mound. This gave a total of 22,580 adult and 13,500 young ants of various ages; 36,080 in all; however, some escaped at the onset, some were away from the mound, and others were not found in the miserable week of labor to pick out the dead ants from the 80 kilos of earth carried off for minute study.

His second method was to visit populous mounds every day, preferably about 11 to 12 A.M. and to collect all the ants that appeared upon the surface of the mound with the aid of a little stick of one centimeter diameter which the ants attacked and mounted till he brushed them off into alcohol, making with seventy-five trials averaging 122 per trial, 9,203 ants in an hour; the next day 9,647, and so on for a week; but by that time the population was so much reduced that the remainder were to be sought by digging into the mound. In some cases, however, it was nearly a month before the population of the mound was exhausted.

Supplementing these domiciliary visits the author also collected the ants found seeking food upon trees and also those ants that were resting in temporary roadside shelters between the nest and the food trees. The author selected isolated ant hills, not any that were connected to perhaps a dozen others with common use of mounds; and he also noted that sometimes the ants disturbed by the census operations may move off in a body as much as 20 metres to some new mound. In such a manner Young obtained a census for no less than five mounds in diverse regions; in size ranging from 45 to 70 centimeters in height and from 95 to 160 centimeters in diameters.

The actual counts of adult working inhabitants of these five mounds were as follows: 19,933; 47,828; 53,018; 67,470; and 93,694. These census figures he regarded as only a beginning, which, he trusts, someone else may continue. Since ants always escaped the census he thinks that the addition of say 10,000 to each of the above would express the real population.

Young emphasizes the wide differences found in mounds of the same ant, one having a population nearly five times that of another. Moreover, there was no correlation between the size of the mound and the numbers of inhabitants. The smallest of these mounds had more than double the population of a much larger mound. The largest mound had scarcely more than half the population of the next to the smallest mound. Young suggested as probable that the smallest population found in a big mound may have been adversely influenced by the mound standing in shade almost all the day and having only two paths to food, in place of seven for the most populous mound.

It being thus shown by Young that these European ants *F. rufa* may inhabit domiciles crowded with from thirty to one hundred thousand adults and that, in one case at least, the young were about half as numerous as the adult workers, and that the numbers could not be inferred from the sizes of the mounds, it remained to be found out how far these numbers hold true for such American ants as *Formica exsectoides* F.

LONGEVITY, NATALITY, AND MORTALITY IN ANTS

The smaller numbers we derived for the American ant might be due in part to the count being at the time of year when there were no young, while the summer counts in Europe allowed for newly arrived adults being reckoned in, for these populations may well rise and fall through a single year according as successful breeding adds to the adult population or as poor conditions lead to rapid loss of adults. This raises the problems of length of life, birth rate, and mortality in these ants.

Unfortunately not much is known about these aspects of ant life. Lord Avebury states that worker ants had been kept by him from 1875 as late as 1881; but this possibility of longevity, great for insects, must be discounted for such large, wandering and very audacious ants as *Formica exsectoides*, exposed to all the risks of free life day and night and moreover working in the summer season at a rate that may be expected to be inimical to long life.

Attempts to keep *Formica exsectoides* in captivity and to make permanent mounds in new localities by frequent transportations of populations and additions of new workers led us to the conclusion that mortality may be great and that conditions of life may be such that communities rather rapidly become depopulated.

Observation of individual mounds through years in the best natural environment shows that some mounds become depopulated and may be deserted, while others increase in population, and yet other mounds hold their own for many years with very little apparent change.

Obviously, to maintain the community, the birthrate should at least be as great as the mortality. The mound serves for the protection of the few perfect females or so-called queens, which are the chief maintainers of the birthrate for the entire community, since the workers for the most part are not directly involved in reproduction.

The number of queens in a domicile is a determining factor in the problem of populations, and one of the most important elements in the maintenance and increase of the population of a mound must be the number of queens added to it. In our mound with 8,228 workers were found but eleven queens, but in another mound very little larger, we found as many as thirty-three queens and very large and populous mounds may be expected to contain even more.

The one queen of the above eleven, taken in May, began to lay in captivity at that season and produced a dozen eggs within three days. In this same species Pierson found that the queens continued breeding throughout the warm season in captivity. In *F. ulkei* the breeding season is only about one month according to Holmquist, who found that in captivity nine queens laid on the average 100 eggs in that season or some three eggs a day as compared with our ant that started at the rate of four eggs a day; even here, however, there is the added variable that one queen laid as many as 190 eggs or nearly twice the average of the nine.

Pierson also found in *Formica exsectoides* that the eggs became mature ants in about one month. If we assign a breeding season of three months with three broods, our eleven queens might add 1,320 adults per month; thus if these did not get killed, there might be some 3,960 new ants in the fall to go into winter quarters. On such basis half of the ants we counted in the winter might have been young ants born in the previous summer. This rate of birth might be offset by a corresponding mortality or it might lead to very rapid increase in the population through years as conditions warranted.

That the yearly increase may be proportionally very great and the mortality very large may also be inferred from the fact that Young counted in *F. rubra* 13,500 young with 36,080 adults, but as all the adults were not then in the mound, the ratio of young and old was doubtless more nearly one to three than one to two.

On the other hand, Eidman, as quoted by Myers, kept in captivity the small ant *Lassius niger* and counted 3,456 adults with 11,600 young;.that is, the young nearly three times the adults; but the ratio of one to three derived from *F. rufa* by Young is doubtless more nearly the truth for *F. exsectoides*, since these ants have so much the same habits and structure.

Our large mound showing some 13,144 young might then have had two to three times as many adults, or from 26 to 39 thousand ants, and were there no mortality the whole population to go into winter quarters might have been as great as forty to fifty thousand ants in place of the ten thousand ants more definitely determined for an average mound.

Since the average mound was very roughly not much over half the dimensions of the very large mound, it might have been expected to have but half the population; except for the important fact that Young found in *F. rufa* no correlation between the size of the mound and the populations; and but for the consideration that the mounds have areas and cubic capacities twice and four times the linear dimensions. Of these two factors, area and capacity, the former is the determining one for the population, since in large mounds the centers are no longer inhabited, while the surface is the real essence of the mound as supplying the sun heat essential for the well-being of the adults and for rearing young populations. We might then have assumed that the big mound should contain four times the population of the average mound of half the height; or forty thousand ants as survivors in winter.

In conclusion, there seems no convincing evidence that the populations of ants in American mounds here in the East are anything like what has been sometimes assumed; being of the order of ten to fifty thousand while the more exact estimates of Young for *Formica rufa* in Switzerland show thirty to one hundred thousand or more as probable.

With the sparse data at hand and considering the great numbers of unknown factors it would seem rash to assume that one of the specific differences between *F. rufa and F. exsectoides* lies in the size of populations, but that might prove to be the case with adequate data. In both cases the populations doubtless rise and fall annually somewhat as in the honey bee and their numbers are comparable with those of the honey bee; while on the other hand there is no reason to assume that these mound builders have such large numbers as half a million, as assumed by Forel and by Avebury, which would make these ant populations approach those of certain termites.

The size of the populations of these large ant mounds has some definite bearing upon the practical problem that these ants are accused of injury to forests: first by aiding the insects that suck juices of trees and secondly by actually killing some small trees near their mounds.

The mounds often occur in settlements, or colonies of few to many. In Baltimore county there is such a colony of some two hundred mounds and in the combined areas of Montgomery and Prince George's counties "infected" we counted 989 of which 127 were then occupied and in Pennsylvania there were at one time 1,600 mounds in one area and 1,800 in another colony, as stated by McCook. With such large numbers of mounds it becomes of importance to know whether the populations in one mound rise to the ten thousand, one hundred thousand, or the half million level.

With an estimated average of some ten

thousand ants in one mound, the Baltimore county colony may present about two million ants and that larger colony nearer Washington some eight million of ants. The statements in literature that such colonies contained hundreds of millions of ants seem to lack present basis of actual counts. Only the taking of an actual census of the ants in many mounds will eventually decide the question as to the average populations existent in these mounds.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

THE GREAT LIFE CYCLE.
By William Irvin Utterback. The author
10 cents *Huntington, West Virginia*
3¾ x 9¼; 2 pp.

It is high time that THE QUARTERLY REVIEW OF BIOLOGY gladdened the hearts of its readers once more with another contribution to its *Fundamentalist Portrait Gallery*. No more worthy candidate for this high honor could possibly be found than William Irvin Utterback, B.S., A.M., head of the department of zoology of Marshall College, Huntington, West Virginia, and author of "The Naiades of Missouri," "The Myth of the Manitou," "Biology and Human Welfare," etc., etc. The individuals who have been included in this series of *Portraits* hitherto have come from various walks of life, chiefly clerical, but we have not before had a professional zoologist, head of the department in a college of around 1500 students, of whom nearly 600 "are enrolled in biologic courses." We emphasize these technical points because they have an important relation to what follows, and because other professional biologists have some time been urging the editors of this REVIEW to give due attention to Professor Utterback's case.

The essence of Professor Utterback's contribution to the problem of organic evolution is exhibited in the full page chart, which is here reproduced with the permission of its author. We recommend its careful perusal. It demonstrates, with devastating clarity, the intellectual level to which the philosophy of reconciliation between science and theology belongs. In embracing this philosophy Professor Utterback does not stand alone. On the contrary he has not a few distinguished associates among professional scientific men, who, along with him, hold that science and theology can, and should be, reconciled. It is desirable for these gentlemen to see precisely the kind of thing this philosophy may lead to, and must lead to if followed through with any degree of thoroughness or persistence.

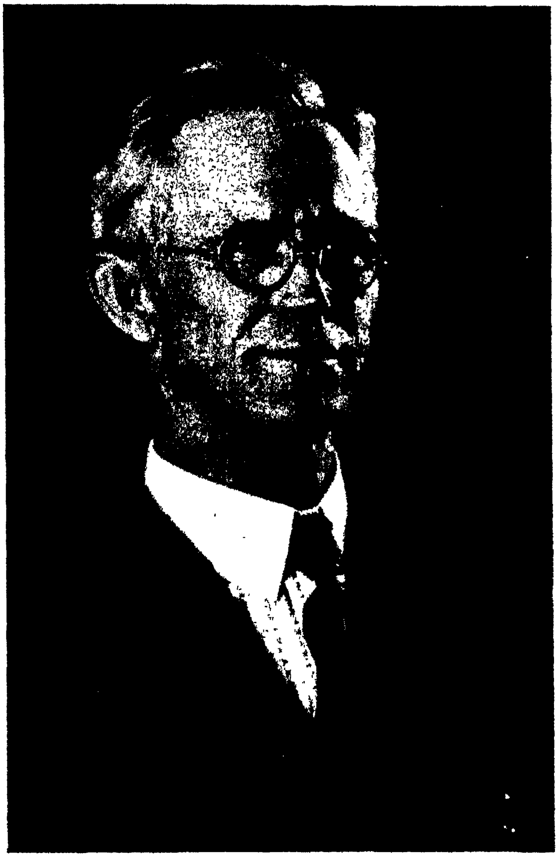
Coming now to Professor Utterback's text accompanying the chart we may first note what he says regarding its provenience.

> No key is necessary in the use of this chart since the arrangement is intended to be self-explanatory if

the reader will start with "FIRE" as the point of construction and will follow the circle clock-wise until he ends with "FIRE" as that of destruction.

Through his many years of scientific and scriptural research the author has endeavored to harmonize the infallible scriptures with true science and also has attempted to project some light into the night of doubt relating to the evolution of man by making some discoveries concerning the origin and the early history of man. Some have said that science has a tendency to weaken our faith in the word and works of Deity, but the author of this chart has had a constant assurance of his faith while spending many years as professor of biology in both denominational and secular colleges. On one occasion the Presbyterian Synod of the State of Missouri honored him by sending him to organize a secondary college in the scene of Harold Bell Wright's famous novel, "The Shepherd of the Hills."

While presenting this controversial subject of organic evolution through newspaper, science journal, lecture room and even the pulpit and Bible class, the author has never been censured as a radical liberalist; however, his compromising views with the leading scientists, theologians and historians in regard to man's origin and destiny should not place him in the very same category with the extreme fundamentalists, yet his leaning may be more in that direction since it is his firm conviction that there is surely nothing to hinder a good biologist from tacking his faith to the supernatural as well as the natural.

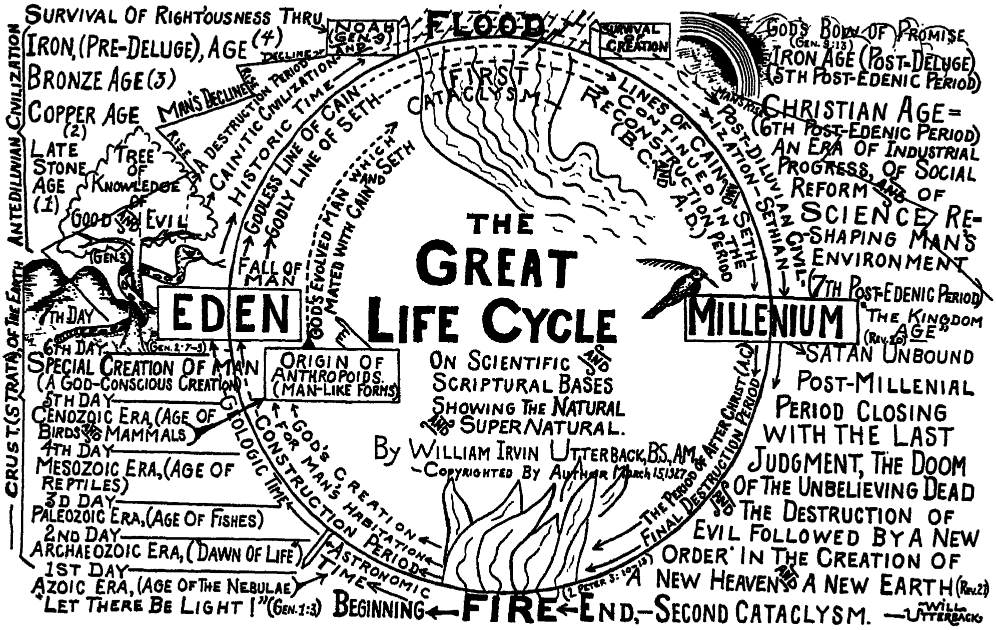


William Irvin Utterback

The accompanying scheme is fashioned on such basis and is considered convincing by the dean of a foremost Divinity school and institute of sacred literature. Therefore, since this viewpoint on evolution also receives the endorsement of scientists and historians, the writer would dedicate it to God and man in acknowledgment of that divine and human love which will usher in a greater day.

The author identifies the fifth day of creation with the Cenozoic Era, and states that mammals, including anthropoids and *Pithecanthropus erectus*, were then brought into being.

Then came the Sixth and Final great Day in God's creation,—that wonderful era, the spirit of which still pervades our modern life. Now that the world was created for Man, a God-conscious man was finally created for the world. This was a super-man created directly by the hand of God in his own image in the


THE GREAT LIFE CYCLE
On Scientific and Scriptural Bases Showing The Natural and SuperNatural.
By William Irvin Utterback, B.S., A.M.
—Copyrighted By Author March 15, 1927
Survival Of Rightousness Thru Noah (Gen. 9)
Antediluvian Civilization
Iron, (Pre-Deluge), Age (4)
Bronze Age (3)
Copper Age (2)
Late Stone Age (1)
Man's Decline
Rise
Decline
Rise
A Destruction Period
Cainitic Civilization
Historic Time
Godless Line of Cain
Godly Line of Seth
God's Evolved Man Which Mated With Cain and Seth
Tree of Knowledge of Good and Evil
(Gen. 3)
Fall of Man
EDEN
Crust (Strata) Of The Earth
7th Day
6th Day (Gen. 2:7-9)
Special Creation Of Man (A God-Conscious Creation)
Origin of Anthropoids. (Man-like Forms)
5th Day
Cenozoic Era, (Age of Birds and Mammals)
4th Day
Mesozoic Era, (Age of Reptiles)
3d Day
Paleozoic Era, (Age Of Fishes)
2nd Day
Archaeozoic Era, (Dawn Of Life)
1st Day
Azoic Era, (Age Of The Nebulae) "Let There Be Light!" (Gen. 1:3)
Geologic Time
God's Creation for Man's Habitation Construction Period
Astronomic Time
Beginning
FIRE
End,—Second Cataclysm.
(2 Peter 3:10-13)
FLOOD
First Cataclysm
Survival of Creation
God's Bow of Promise (Gen. 9:13)
Lines of Cain and Seth Continued in the Reconstruction Period (B.C. and A.D.)
Man's Rise
Post-Diluvian Civilization—Sethian
Iron Age (Post-Deluge) (5th Post-Edenic Period)
Christian Age = (6th Post-Edenic Period) An Era of Industrial Progress, Of Social Reform and of Science Re-Shaping Man's Environment
(7th Post-Edenic Period)
MILLENIUM
"The Kingdom Age" (Rev. 20)
Satan Unbound
The Period of After Christ (A.C.) and Final Destruction Period
Post-Millenial Period Closing with the Last Judgment, The Doom Of The Unbelieving Dead and The Destruction of Evil Followed By A New Order In The Creation of A New Heaven and A New Earth (Rev. 21)
—Will Utterback

The Accompanying Chart is An Attempt To Show The Past, Present and Future. No Key is Necessary For its Use Since The Arrangement is Intended To Be Self-Explanatory if The Reader Will Start With "Fire" as The Point of Construction and Will Follow The Circle Clock-Wise Until He Closes With "Fire" as The Point Of Destruction.

* * * * * *

The Geologic, Historic and Future Periods Of Time Are Presented Within This Great Life Cycle As Mostly Determined On The Scriptural and Scientific Bases As Well As On Facts Gained Through The Natural and The Super-Natural

* * * * *

The Essential Features Of This Presentation Are That Of The Mating Of God's Specially Created Man With His Evolved Human Form Followed By The Cainitic and Sethian Civilizations.

* * * * *

The Mingling Of The God-Conscious With The Evolved Man Solves That Age-Old Problem Of "Who Were The Wives Of Cain and Seth"? Without Encroachment Upon Orthodoxy

All Forms Of Life Are Cycles

The Above Illustrated Conception Is An Attempt To Compromise Modern Views Of The Scientist, Theologian And Historian.

In This Grand Race Course The Great Epoch Of Fire Is The Goal For Jehovah,—The Creator, And Satan,—The Destroyer.

Four Parallels Are Seen Here In The Cataclysms Of Fire And Flood, And In The Peaceful Periods Of Eden And The Millenium,—All Bounding Four Long Eras Alternating In Their Construction And Destruction.

As To The Time Element Covered By This Great Scheme The Divisions Are Compromised Estimates Of Great Scholars and May Indicate Ten Billion Years Ago For Astronomic Time, One Billion Years For The Geologic Time, Ten Thousand For Historic Time, And, Judging From The Known Past, Twenty-Five Thousand Years For Future Time

* * * * *

According To Most Commentators The "Days" Of The Genesis Cosmogeny Are The Geologic Ages Whose Pages Are Plainly Read In God's Other Great Text, His Wonderful Earth-Book.

The Finite Mind Of Man Is Unable To Fathom The Extent Of The First Great Day When Our Earth May Have Functioned As A Luminary In The Universe.

The Present Highly Heated Interior Of The Earth Is Positive Proof That The First Creation Was Conceived In Fire By The Great Creator Who Espoused The Cause Of Self-Existent Rightousness With All Its Attributes; However, Fire Was Made Destructive In The Hands Of Satan Who Championed The Cause Of Self-Existent Sin With Its Attending Attributes.

Yet God-Almighty Is The Greater Power!

* * * * *

Satan's Power May Have Prevailed In The Pre-Deluge Periods Of The Late Stone, Copper, Bronze and Iron Ages Of The Post-Edenic Time, But God's Power Was, Is and Will Be, Dominant Throughout The Iron Age (Post-Deluge) and Christian Era Of Pre-Millenial Time.

* * * * *

The Crowning Age Of Love and Peace,—The Great Millenium,—Will Stand In The Same Constructive Relation As Eden Did To Its Six Geologic Ages Since It Will Come At The Close Of Six Historic Ages.

Symbolically Another Week Of Six Labor Days Shall Have Been Closed With The Seventh Day (Millenium), As The Rest Day,—An Age When Love Will Predominate

* * * * *

Then Will Come The Post-Christian Age, When, As In All Life Cycles, The Great Decline Will Begin Where The Most Productive Life Ends and After A Long, Final Conflict With Evil There Will Come "The Day Of Jehovah-God" When The Great "Alpha and Omega,—The Beginning and The End,"—Will Be Given The Victory In That "The Elements Will Melt With Fervent Heat" Followed By A Reign Of Rightousness Without Its Sting Of Death Throughout Another Great Life Cycle.

> midst of perfect conditions,—a Paradise, or Eden. Here at last the great Creator had succeeded in establishing an innocent triune Man upon the earth where, at first, effective bars were erected against the destructive force of Satan.

The remainder of the story of human evolution runs as follows, according to Professor Utterback:

> Just as fire was the beginning and will be the end of one Great Life Cycle, or Phylogeny, so in the dust of the earth is the beginning and the end of the individual, or Ontogeny, of man. The earth was cursed for man's sake since it is better for fallen men to struggle with the stubborn earth than to live without toil and thus the great pronouncement was made: "In the sweat of thy face thou shalt eat bread, till thou return unto the ground; for out of it wast thou taken; for dust thou art and to dust shalt thou return." However—
>
> "Dust thou art to dust returnest
> Was not spoken of the soul."
>
> Yet the first representatives of God-conscious man, after yielding to the general sin of disobedience in tasting of "the tree of knowledge of Good and Evil," fell toward the level of those anthropoids who had dwelt outside of Eden and had now evolved to a primitive form of the genus Homo, represented by the highest types of Neanderthal Man, (*Homo Neanderthalensis*), and even by the Cro-Magnon type, the earliest form of Modern Man, (*Homo sapiens*). Outside of Paradise, at the time of the expulsion, the world was doubtless passing through a transitional period from the old stone age (Paleolithic) to the late stone age (Neolithic) which marks the beginning of modern man.
>
> According to writers who are neither extreme fundamentalists, nor radical liberalists, the Genesis cosmogony is not in conflict with that of science and these same theologians who accept creation as expressed indirectly through natural laws and directly through a Divine Hand, that is, naturally and supernaturally, also interpret the following as the antedeluvian (*sic*) civilization:
>
> "There were giants in the earth in those days; and after that, when the Sons of God came in unto the daughters of men and they bare children to them, the same became mighty men which were of old, men of renown."
>
> Evidently the "Sons of God" were Seth, and even Cain with all his sin,—the sons from God's special creation into whom the "breath of life" had been breathed; and the "Daughters of Men" were plainly those human forms from God's evolved creation. There is no definite account in God's infallible word that Adam and Eve were parents of daughters bearing names as did their sons and, even if it were true that they enjoyed such parenthood, it is unthinkable that their sons took for their wives their own sisters. Neither is there any scriptural record that the wives of Cain and Seth were fashioned from the bodies of these sons of Adam just as their mother was begotten from their father's rib.

This, we think, will be enough, indeed a plenty. No "reconciler," whether biologist, physicist, or parson, should be without a copy of Professor Utterback's handy pamphlet. We find it difficult to conceive how anything more completely suited to their purpose could be found. In current phraseology, it is swell.

EVOLUTION BY SYMBIOSIS.

By H. Reinheimer. *Grevett and Co., Ltd.*
15 shillings net *Surbiton, England*
4½ x 6⅞; 141

We have had occasion in these columns to give considerable attention to the productions of paradoxers, and have found the opportunity to point out the entertainment and instruction they frequently contain. The *opus* under consideration here, which is of the same genus but a different species from those previously noticed, cannot, we are sorry to say, be similarly recommended. It labors the thesis that the unmoral struggle for existence which biologists allege lies at the basis of evolution is perversely conceived, and that symbiotism and coöperation are really its guiding rule. The evidence given for this generality is frail, and, what is much worse, is advanced with a terrible earnestness that deprives it of the all saving grace of humor.

OLD MOTHER EARTH.

By Kirtley F. Mather.

Harvard University Press
$2.50 5½ x 8; xiv + 177 *Cambridge*

This book has developed out of a series of radio talks on geology given by the author at Boston in 1927–1928. Naturally it is for the general reader. Not only geology but the origin of life and the evolution of mankind are presented in an engaging manner. The text is enriched by 61 illustrations.

* * *

GENETICS

DAIRY CATTLE BREEDS. *U. S. Department of Agriculture Farmers' Bulletin No. 1443.*

By Amer B. Nystrom.

Government Printing Office
5 cents *Washington, D. C.*
6 x 9½; 29 (paper)

In this bulletin are discussed the number and distribution of the different dairy breeds in the United States, their origin and development and the chief characteristics of each. Suggestions are included concerning the factors to consider in selecting a breed. With the description of each breed a scale of points for a cow in use by the breed association is given. There are twenty-one illustrations of famous bulls and cows and a number of tables exhibiting the butter-fat and milk production of pedigreed animals.

* * *

THE LIVESTOCK REVIEW FOR 1927. *United States Department of Agriculture Miscellaneous Publication No. 28.*

By H. M. Conway.

Government Printing Office
10 cents *Washington, D. C.*
5¾ x 9⅛; 44 (paper)

"This review is designed (1) to give a perspective of basic conditions in the livestock industry, (2) to point out and emphasize the short-time variations and the general trend of market supply and demand and resulting prices during 1927, (3) to present a general interpretation of the livestock situation, and (4) to indicate the basis for some of the statements appearing in The Agricultural Outlook for 1928."

* * *

GENERAL BIOLOGY

BIOLOGICAL CHEMISTRY AND PHYSICS OF SEA WATER.

By H. W. Harvey. *The Macmillan Co.*
$4.25 5½ x 8½; x + 194 *New York*

This useful treatise, written to fill the gap in oceanographic literature between the publication of *The Depths of the Ocean* in 1912 and the beginning of current bibliographies in 1926 in the *Journal du Conseil International pour l'Exploration de la Mer*, will be found interesting by the general biologist as well as the specialist in oceanography. It discusses the sea as the environment of plants and animals, maintaining throughout a primarily biological viewpoint, though the details of the discussion are of physical and chemical matters. The topics treated are: Chemistry of sea water; water movements (tides and currents); temperature of the sea; color and illumination of sea water; chemical and physical factors controlling the density of population. There are bibliographies for each of these topics.

* * *

NATURAL HISTORY OF CANTERBURY. *A Series of Articles on the Early History of the Province and on the History of*

Scientific Investigation, up till 1926, as well as on some Results of this Investigation.
Philosophical Institute of Canterbury
17 s. 6 d. *Christchurch, New Zealand*
5¼ x 8; 299

Canterbury Province of New Zealand—a natural unit in that it is between high mountains on one hand and the sea on the other and has a special climate and geological history—has been the leading agricultural area in New Zealand ever since it was founded seventy-five years ago. In this volume The Philosophical Institute of Canterbury has issued a series of articles on the early history of the Province and on the history of scientific investigation up to 1926, as well as on some results of these investigations.

It was on a sheep farm in the sub-alpine region of Canterbury that Samuel Butler dwelt for four years, obtained the background of Erewhon, and carried on his controversy with the Bishop of Wellington. It was in this region also that Robert Brown, a shoe maker by trade in Glasgow until the age of 52, made his intensive studies of mosses and ferns, his equipment being an old-fashioned microscope and a home-made camera lucida. Sir Julius von Haast, the geologist, who lived here from 1860 to the time of his death in 1887, contributed many articles on the geology of Canterbury and was founder of the museum. Frederick Wollaston Hutton, in his early years a geologist, worked chiefly in New Zealand on zoology and the geographical relations of the New Zealand fauna.

It is around such pioneers as these that the book is written. The articles have been made as free of technicalities as possible in order that the lay reader would not find the book forbidding. Since each contributor is an authority in his field the book contains much information that is not otherwise accessible to the student of natural history. There is a table of contents and 27 illustrations, but unfortunately no index, which decidedly reduces its usefulness to the student.

◆

METHODIK DER WISSENSCHAFTLICHEN BIOLOGIE. *Erster Band: Allgemeine Morphologie. Zweiter Band: Allgemeine Physiologie.*
Edited by T. Péterfi. *Julius Springer*
188 marks (paper) for two volumes *Berlin*
198 marks (cloth) for two volumes
6¾ × 10¼; Vol. I, xiv + 1425
Vol. II, x + 1219

This large treatise on biological technique is stated by the editor to be needed in addition to the great Abderhalden *Handbuch* on the same subject because the latter is too large and too detailed. Doubtless the present work will serve a useful purpose, particularly for laboratories which cannot afford to purchase the larger work. Even for these, however, it will be no easy task to buy this treatise. Its price in paper is approximately $47. Our guess is that few American laboratories except the larger ones will feel that they can afford it.

The material is divided between the two volumes on the basis of morphology and physiology. The separate chapters are contributed by some forty odd specialists. The choice of subjects is good and the editing has been well done. Wherever we have had occasion to consult it in connection with the routine work of the laboratory we have found the indexing so good as to make it possible quickly to find what is wanted, and the information has been presented in sufficient detail to be practical. We congratulate the editor, Dr. Péterfi, on his enterprise in putting through so considerable a task so well, but we wonder at the economics of the business. Perhaps the law of diminishing returns no longer operates in Germany.

THE SOCIAL INSECTS. *Their Origin and Evolution.*

By William Morton Wheeler.
Kegan Paul, Trench, Trubner and Co., Ltd.
21 shillings net *London*
5½ x 8½; xviii + 378

The French edition of this notable book was reviewed *in extenso* in The Quarterly Review of Biology by Professor Philip P. Calvert (Vol. II, pp. 119–124). The author states that:

> In preparing this English edition I have retained the original lecture form, but several passages, which had to be omitted in order to bring the volume within the requirements of the French publisher, have been restored to the text, a number of typographical and other errors have been corrected and a small amount of new material has been added. I have also introduced several new illustrations and have omitted a few of those in the French edition. In its present form the work has been brought up to date so far as this was possible without unduly expanding the text and the bibliography.

It is a great service to biology to have this learned and entertaining volume available in English.

THE SEAS. *Our Knowledge of Life in the Sea and How it is Gained.*

By F. S. Russell and C. M. Yonge.
Frederick Warne and Co., Ltd.
12 s. 6 d. net *London*
4½ x 6⅛; xiii + 379

This attractive "handy volume" with its numerous illustrations (there are 384, of which 167 are in full color) will be particularly interesting to the lay reader whose hours of recreation are spent near or on the sea. The authors, both of whom have been connected with the Marine Biological Association at Plymouth, England, have a wide acquaintance with the fauna and flora of the ocean. Within the covers of this book they give the best popular account of oceanography, in its broadest sense, that we have seen. The illustrations are largely new and well chosen. If the book were to appear devoid of text it would still be well worth possessing because of them. There is an index.

JAHRESBERICHT ÜBER DIE WISSENSCHAFTLICHE BIOLOGIE. *Zugleich Bibliographisches Jahresregister der Berichte über die Wissenschaftliche Biologie. Band I.*

Edited by Tibor Péterfi. *Julius Springer*
69 marks *Berlin*
7 x 10¼; xii + 627 (paper)

The first volume of a new bibliographic enterprise, of interest to all biologists. It lists the biological titles from some 1328 journals of all parts of the world. All titles listed are of the year 1926. The typographical treatment is good; each title so far as possible apparently carries the useful item of the author's address; there is good cross-referencing. We confess to liking the classification better than that of *Biological Abstracts* in a number of particulars. Altogether we are inclined to predict that this new *Jahresbericht* will succeed if it maintains its initial standard.

THE IDEA OF MEMORY IN BIOLOGY. *Being the Tenth Earl Grey Memorial Lecture Delivered at King's Hall, Armstrong College, Newcastle-on-Tyne, March 2, 1928.*

By E. W. MacBride.
Oxford University Press.
35 cents 6 x 9; 27 (paper) *New York*

Professor MacBride, as every one knows, is an ardent Lamarckian. This lecture is about the inheritance of acquired characters. It chiefly discusses the experiments of Dürkhen and Heslop Harrison upon the coloration of insects; color and other adaptations of amphibia; and some of the recent work in experimental embryology, notably that of Spemann. The odd thing is that in this whole lecture devoted to the idea of memory in biology not one single mention is made of either Hering, Samuel Butler, or Semon! And what is perhaps still odder is that a careful perusal of the lecture fails to discover in it one single "idea" about memory in biology which has not already been discussed in one form or another by one or more of these three persons.

AN INTRODUCTION TO OCEANOGRAPHY. *With Special Reference to Geography and Geophysics.*

By James Johnstone.

Hodder and Stoughton, Ltd.
15 shillings net *London*
5½ x 8½; xi + 368 + 4 maps

This revised edition of Professor Johnstone's outline of oceanography should be of interest to a wide range of readers. There are chapters on the origin of the oceans, the depths of the ocean, the sea bottoms, the oceanic margins, the chemistry of sea water, the physical characters of sea water, the tides, the oceanic circulation, and secular changes in the ocean. The treatment is general, and the attempt has been to provide an introduction to all the important aspects of oceanography. There is an appendix giving a list of the principal authorities consulted, and a good index.

KRITISCHE THEORIE DER FORMBILDUNG. *Abhandlungen zur theoretischen Biologie. Heft 27.*

By Ludwig Bertalanffy.

Gebrüder Borntraeger
14 marks *Berlin*
6⅝ x 10; vi + 243 (paper)

A critical discussion of the present state of knowledge of morphogenesis, prefaced by a hundred pages regarding theoretical biology in general. The general conclusion reached is that there is no evidence in what we know of embryonic development for the existence of any specific form producing or controlling factor. Form, on the contrary, is a *primary* characteristic of living organisms. This is a well written, interesting and stimulating discussion of the fundamental problems of biology.

MEASUREMENT OF SALINITY OF SEA WATER. *Department of Commerce, U. S. Coast and Geodetic Survey Special Publication No. 147.*

By Jerry H. Service.

Government Printing Office
10 cents *Washington, D. C.*
5⅞ x 9¼; iii + 20 (paper)

In this publication is presented the preliminary calibration of the dipping refractometer as well as a study of other methods available for use on board ship for measuring the proportion of total dissolved solids in sea water. In the text are 8 illustrations, 3 charts and 5 tables.

FUNDAMENTALS OF BIOLOGY.

By Arthur W. Haupt. McGraw Hill Book Co.
$3.00 5⅝ x 9; xii + 358 *New York*

This elementary text for the use of beginning classes in general biology soundly follows conservative lines. Roughly half the book deals with morphological matters, and the rest with such general topics as genetics, ecology, evolution, etc. It is sufficiently well illustrated and indexed.

GENERAL BIOLOGY.

By Leonas L. Burlingame, Harold Heath, Ernest G. Martin and George J. Peirce.
Henry Holt and Co.
$3.50 5½ x 8½; xxx + 597 *New York*

A text book for use in an introductory course for college students. It is planned on the idea of stressing principles rather than factual details, and demands very little equipment in the collateral sciences for its comprehension.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN Lieferung 271. *Einrichtung von Zimmer- und Freiland-Aquarien und -Terrarien einschliesslich der Technik der Haltung und Zucht von Fischen, Reptilien und Amphibien.*

By Wilhelm Klingelhöffer.
Urban und Schwarzenberg
24 marks 7 x 10; 456 (paper) *Berlin*

This fascicle of the Abderhalden handbook contains by all odds the most thorough and comprehensive discussion of small aquarium and terrarium technique that we have seen.

THEORETISCHE BIOLOGIE.

By J. von Uexküll. *Julius Springer*
15 RM (Paper) *Berlin*
16.80 RM (Cloth)
6⅝ x 9½; x + 253

The first edition of this book, in English translation, has been noted in this Review (Vol. II, No. 2). This issue, *gänzlich neu bearbeitet*, does not appear to contain anything essentially new.

PLANKTONKUNDE. *Eine Einführung in die Ökologie der im Wasser Schwebenden Kleinwelt.*

By Wilhelm Heesen. *Otto Salle*
2.80 marks 5½ x 7½; xi + 90 *Berlin*

A very satisfactory little text designed as introductory to the study of plankton. For further investigation a list of more exhaustive references is provided.

BLOOD. *A Study in General Physiology.*

By Lawrence J. Henderson.
Yale University Press
$5.00 6 x 9; xix + 397 *New Haven*

A long review of this notable book will appear in the next number of The Quarterly Review of Biology.

HUMAN BIOLOGY

THE TWILIGHT OF THE AMERICAN MIND.

By Walter B. Pitkin. *Simon and Schuster*
$3.00 5⅝ x 7⅞; xviii + 362 *New York*

The orthodox eugenic creed contains two main articles: first, that the inferior sorts of men should be discouraged, perhaps forcibly restrained, from breeding, and second, that the superior sorts of men should be encouraged to breed more rapidly. There is here a threat and a promise: unless we subscribe to Article 1, the world will be entirely populated by morons in 1987, or some such date;

and if we subscribe to Article 2, the average man of 1962 will possess Galton's I.Q., Voltaire's literary style, Schubert's musical talent, and so on.

The present volume is not concerned with the first of these canons, nor does it deal with the possibility of carrying the second into execution. The author limits himself to the question of whether it is really desirable to produce a great many more highly intelligent people than now exist; and he deals with this question purely on the basis of finding jobs for these superior people. He makes, in short, a survey of the various occupations of the United States, and estimates the number of jobs which require high intelligence if they are to be done properly. His conclusion is that we already have a surplus of intelligence, and that this surplus is growing, not shrinking; and we believe that he has pretty well backed up his conclusion with sound evidence as well as clever and amusing dialectic.

We suspect that this book will be very lightly esteemed by the eugenists, but we commend it highly to their earnest consideration. For it poses a number of questions which no eugenist who wants to be considered as more than a mere uplifter can afford entirely to neglect. Pitkin's view of the direction of evolution of society seems to us in general sound: namely, that society is requiring less and less intelligence to keep it going. If this is so, what is the evolutionary use of trying to increase the number of highly intelligent people?

Finally, we may remark that Pitkin's technique has a much wider application than merely to a particular phase of eugenic propaganda. It may, we think, be applied to the uplift in any of its forms. In short, no program of the uplift is worth the paper it is written on unless it is based on a realistic consideration of all the relevant facts, and unless it includes a realistic study of all the consequences which may follow from its adoption. So far as we know, no uplifter has ever presented that kind of program; and we do not expect that any uplifter ever will.

* * *

THE PROMOTION OF THE WELFARE AND HYGIENE OF MATERNITY AND INFANCY. *The Administration of the Act of Congress of November 23, 1924. Fiscal Year Ended June 30, 1927. U. S. Department of Labor Children's Bureau Publication No. 186.*

Government Printing Office
25 cents *Washington, D. C.*
5⅞ x 9¼; vi + 150 (paper)

This volume reached the editorial desk along with the editorial income tax blank; not unnaturally. Therefore, we have made an attempt to discover just what has actually been accomplished by the operation of the Sheppard-Towner Act. On pages 2 and 3 we find a table which shows a total of $4,697,234.86 of Federal funds accepted by the states. This, however, is not the full amount spent, since under the Act most of this must be matched dollar for dollar by the states. The total of Federal and State expenditures we work out to be something over eight million dollars.

Eight million dollars seems to us like a lot of money; what have we got for it, outside of creating some pleasant places for jobholders? Examining the succeeding tables, we find that during the year ended June 30, 1927 there were held a total of 33,783 conferences at which 29,041 mothers and expectant mothers and 227,733 children were registered, inspected, advised, and instructed. In the same period there were also conducted 1196 classes in which 26,356 mothers were enrolled, etc.; that a total of 18,207 talks and lectures, including 110 radio broadcasts, were given to 408 physicians, 794 nurses, 13,442 laymen, and the uncounted millions of the radio audience; that 46,217 sets of prenatal letters were sent out; and that the total of "pieces of literature distributed" was 4,403,218.

We see that the jobholders have not been idle; and it was with something of a thrill that we turned to the section "Some Results of Five Years of Work." Here, said we, we shall learn what all this has accomplished. So we looked eagerly through some remarks about "Expansion of Activities" and "Increase in State Appropriations for Child-Hygiene Work," until we come to the heading "Reduction in Infant Mortality." Here we are given a table which really shows what we want to know. It gives the average infant mortality rates by states for the years 1917–1921 (exclusive of 1918) and 1922–1926—before and after the act took effect. Further, we are able to compare the course of affairs in the coöperating states with those not coöperating. No averages are given in the table, but it is easy to compute them; which we did, with the result here given:

	Infant mortality		
	1917–21 (1918 omitted)	1922–26	*Percent decrease*
16 coöperating states	80.07	71.56	10.6
5 non-coöperating states	84.96	73.18	13.9

This result, we may say, distressed us greatly; and accordingly we tried to see what could be done about it. Our figures are simply flat averages of the rates given in the table; but we have also tried weighting them by the population of the states, and we have tried omitting certain states which either did not come into the Birth Registration Area until 1919 or which did not begin coöperating until 1923. However, no treatment of the figures has altered the conclusion which we should draw from the table above—namely, that eight million dollars of the tax payer's money has been spent with precisely no effect at all on the course of infant mortality.

* * *

AN INTRODUCTION TO THE STUDY OF SOCIETY. *An Outline of Primary Factors and Fundamental Institutions.*

By Frank H. Hankins. The Macmillan Co.
$4.00 5½ x 8½; xiii + 760 *New York*

A text book for use in a general survey course in sociology. It covers, as one might expect, a great deal of ground, much of it properly belonging to other sciences; and it is not to be expected that specialists will agree in all cases with the author's use of material from their fields. He has plainly endeavored to maintain a properly dispassionate and scientific attitude toward human problems, but occasionally slips into pious hopes for uplifting the race. There are, after all, few writers with the detachment of Pareto—who, incidentally, is not mentioned in this book.

Some of the "questions for discussion and further study" appended to the various chapters are, we should say, tall orders. For example, the following from Chapter VII. p. 318;

4. What is the selective value of war?
5. Suggest a practical plan for greatly reducing the proportion of morons in our population.
9. How is selection related to vestigial organs? How would you explain the blindness of fishes living in caves?
12. Is modern charity and philanthropy justifiable?
15. In what ways and to what extent does a race acquire immunity to germs and diseases to which it is constantly subjected?
16. What are the causes of the decline in the birth rate in the past fifty years?
19. Why should births following a war show an unusual proportion of males?

20. If it could be proven that alcohol acts selectively so as ultimately to produce a race immune to its effects, would this warrant its unrestricted use in modern society?

There are references following each chapter; those for chapter VII are the following:

SUGGESTED READINGS

Davis-Barnes: *Readings in Sociology*, pp. 398–480.
Bushee: *Principles of Sociology*, Chap. 24, pp. 386–413.
Carr-Saunders: *The Population Problem*, Chaps. 5, 7, and 11, pp. 88–105, 135–161, and 270–307.
East: *Mankind at the Crossroads*, Chaps. 5, 6, 8, and 9, pp. 110–198 and 231–283.
Holmes: *Trend of the Race*, Chap. 8, pp. 181–204.
———: *Studies in Evolution and Eugenics*, Chaps. 7–9 and 11, pp. 134–169 and 179–188.
Newman: *Evolution, Genetics and Eugenics*, Chaps. 17 and 19, pp. 237–249 and 276–293.
Wiggam: *The Fruit of the Family Tree*, Chap. 18, pp. 304–316.
Wolfe: *Readings in Social Problems*, Chaps. 1 and 2, pp. 17–117.
Wright: *Population*, Chaps. 2 and 6, pp. 20–39 and 99–118.

ADDITIONAL SELECTED REFERENCES

Carr-Saunders: *Population*, entire.
Castle: *Genetics and Eugenics*, Part IV, pp. 331–375.
Darwin: *The Need for Eugenic Reform*, Chaps. 17, 18, and 22, pp. 295–327 and 391–415.
East: *Heredity and Human Affairs*, Chap. 13, pp. 247–265.
Lennes: *Whither Democracy?*, Chaps, 7–9, pp. 252–332.
Popenoe and Johnson: *Applied Eugenics*, Chaps. 6, 8, and 9, pp. 116–146 and 167–183.
Siemens: *Race Hygiene and Heredity*, Chap. 10, pp. 130–154.
Sorokin: *Social Mobility*, Chaps. 10–13, pp. 215–333.

Without disrespect to these authors, we should like to know how many of these questions students will find answered. In fact we should like to have the answers to one or two of them ourselves.

* * *

COMING OF AGE IN SAMOA. *A Psychological Study of Primitive Youth for Western Civilization.*

By Margaret Mead.

William Morrow and Co.
$3.00 5¼ x 8; xv + 297 *New York*

This book has been a "best seller," in spite of the fact that it was written as a serious contribution to anthropology, done under the auspices of the National Research Council, and introduced by Professor Franz Boas. Its large popular sale has been due, we incline to think, to two causes: it is well written, and there is a lot in it about sex.

Looked at solely as a piece of research the first point to be noted is that Miss Mead spent altogether nine months in Samoa, six months of them upon the little island of Taū in the Manu'a Archipelago. During this time she had to learn the language, and collect the data for the study, which included the most extensive probing into the intimate private lives of all the women and girls, and some of the men, in three villages. Doubtless the Samoan language is an easy one to learn, and evidently Miss Mead must be an extraordinarily facile linguist, but making all allowance in both these directions one can but marvel at the range of material covered in the research. When one recalls the testimony of such men as Westermarck and Stefansson for example, that only after years of living with natives did they *really* get "inside" their lives and thoughts it raises a query as to whether Miss Mead penetrated as deeply into the secrets of the Samoan ladies as she thought she did.

The main point brought out by the study is that girls in Taū have fewer inhibitions about sex, and various other crudely biological matters, than do girls in the United States. Broadly speaking, this is no doubt true. But what, precisely, of it? Social customs and attitudes are, taken by and large, adaptive responses to the whole biological and physical environment. When they cease to be adaptive they are apt to change. The sex behavior of the girls and boys of Taū would be less well adapted to a New York City present day environment than is that of the youth of our great metropolis. In spite of the author's rather prolix exposition of her moral judgments and wishes in the matter, we make bold to doubt if the behavior of either group is likely to be very helpful in guiding the behavior of the other.

With the reservations which have been suggested as to the degree of seriousness with which the book is to be taken as a piece of scientific research, we can recommend it heartily as entertaining reading.

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ARCHÆOLOGICAL INVESTIGATIONS IN KAMCHATKA. *Carnegie Institution of Washington Publication No. 388.*

By Waldemar Jochelson.

Carnegie Institution of Washington
$2.75 (paper) *Washington, D. C.*
$3.75 (cloth)
9⅛ x 11½; viii + 88 + 19 plates

This publication, together with a previous one on Archaeological Investigations in the Aleutian Islands, also issued by the Carnegie Institution of Washington, represents part of the results of an investigation carried on by the author in 1910–11 under the auspices of the Imperial Russian Geographical Society. The present volume deals very largely with the implements, weapons and pottery of the early Kamchadal inhabitants, but in addition there is a discussion of the history of Kamchatka and the Stone Age in Siberia and adjacent countries. The author hesitates to link his findings up with any particular age or era. He concludes that during the early Kamchadal history the country was densely populated, the inhabitants living during the winter months in pit-dwellings (abodes in the earth) and in summer in huts on piles several meters high.

There are numerous illustrations of the objects excavated, these coming very largely from pits in the vicinity of Kuril Lake.

In addition to the 19 plates and a map of Northern Asia exhibiting the distributions of palaeolithic, neolithic, bronze and iron stations of Siberia there is a lengthy bibliography and index. The volume is issued in superb form.

* * *

HUMAN MIGRATION AND THE FUTURE. *A Study of the Causes, Effects and Control of Emigration.*

By J. W. Gregory.

Seeley, Service and Co., Ltd.
12 s. 6 d. 5½ x 8½; 218 *London*

The central thesis of this book is that human migration is beneficial, both to the countries that lose and to those that receive the wanderers. The distinguished author, who is Professor of Geology in the University of Glasgow, argues that there is still plenty of room in temperate regions of the globe for all those who want to emigrate from European countries. In his view migration offers something approaching a solution of the world population problem. He discusses birth control only as an alternative to emigration, and appears to regard it with disfavor. He hopes that "the European race may not be forced to methods of birth control that would increase its numerical inferiority to the coloured races."

The book is well documented and indexed, and will interest all students of human biology.

THE INTERPRETER GEDDES. *The Man and His Gospel.*

By Amelia Defries. *Boni and Liveright*
$3.00 5½ x 8½; xiii + 334 *New York*

Patrick Geddes is without doubt one of the most remarkable men of our times. Many years ago when the reviewer was a graduate student Geddes spent a morning with him watching and discussing the experiments in progress, and the memory of his eager, vivid personality has always remained fresh. His versatility has been extraordinary. As biologist, sociologist, botanist, philosopher, town planner, and all-round human being he has everywhere left his mark.

To our taste, at least, this book does not do Geddes justice. Somehow he would seem to deserve something better biographically than the turgid adulation of a very feminine hero-worshipper. However, in the absence of anything better, all biologists will be interested in reading this. Some idea of the wide range of Geddes' interests may be gained from the chapter headings, which are as follows: The Masque of Learning; The Cities and Town Planning; The Outlook Tower; The Returning Gods—Olympus; The Notation of Life—Parnassus; Geddes in his Garden; A Botanist Looks at the World; Art and Sex; Cities in Devolution; Education, Politics, Housing; Scotland and France; Jerusalem; Montpellier; Last Words; Five Friendly Critics.

There is a foreword by Rabindranath Tagore, a preface by Lewis Mumford, and an introduction by Israel Zangwill. A selected bibliography of Geddes' writings ends the book. There is no index.

* * *

THE FORMATION OF THE CHINESE PEOPLE. *An Anthropological Inquiry.*

By Chi Li. *Harvard University Press*
$5.00 7 x 10¼; 285 *Cambridge*

This book is an attempt to determine the origin of the modern Chinese through anthropological, archaeological, and historical investigations. The author begins with a study of the physical traits of the modern Chinese. He then investigates the building of city walls in different provinces, with the general thesis that the earlier the period of greatest building activity, the earlier was the occupation of the province by the Chinese. He then investigates the origin and migration of the Chinese as indicated by the locality of occurrence of ten typical surnames. He then considers the barbarians with whom the Chinese have been in contact, and their relations with the Chinese. In a final chapter he considers the various elements whose integration has resulted in the modern Chinese.

It is not always easy to follow the author's argument, partly because his expression is not as clear as might be wished. We own to a certain scepticism as to the value of some of his results, especially those based on the history of surnames; but our ignorance of things Chinese prevents our expressing a critical judgment on most of the book. It is fair to say, however, that the author has been quite ingenious in developing statistical methods for handling his historical material.

The book seriously lacks an index.

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SECONDARY SCHOOL EXAMINATION STATISTICS. *Prefaced by a Simple Introduction to Statistical Methods.*

By J. M. Crofts and D. Caradog Jones.
Longmans, Green and Co., Ltd.
$1.00 4⅞ x 7½; 88 *New York*

A brief account of the machinery of School Certificate Examinations in England, with some statistical discussion of the results. There is an excellent introductory chapter on the statistical analysis of examination results, written especially for the non-statistical reader; and chapters on the School Certificate and Higher School Certificate examinations. The analysis indicates that at age 16

> the average girl is the equal, if not the superior, of the average boy, but that taken all round girls show less variation than boys. They may be regarded in the mass as more steady or more humdrum, according as we wish to be complimentary or otherwise. At the stage of the Higher School Certificate two years later—that is, roughly, at about 18½ years of age—the difference in variability has increased, and the superiority previously shown by the girls in certain subjects has vanished altogether, while in others it shows signs of decreasing, indicating that girls cannot compete on equal terms with boys in academic tests of the standard in question. But it is important to note that this is only true of boys and girls in general: there appear from time to time exceptional girls who can on equal terms, compete with and beat the best boys of their year at least in some subjects.

THE SOCIOLOGY OF LIFE INSURANCE.

By Edward A. Woods. D. Appleton and Co.
$2.50 5¼ x 8; xix + 331 *New York*

The title of this book is misleading. It actually consists of high-toned language for the insurance salesman. A sample:

> The idle rich and the thriftless masses are the menace of any nation. They were in Babylon, Assyria, Persia, Greece, and Rome in antiquity, and in France at the time of the Revolution. They are even so in America to-day.
>
> A great institution that is encouraging more than a majority of the entire population to practice systematic thrift over a long period of years or a lifetime and so to form habits that foster other ways of saving is of great social, economic, and even spiritual value to the nation.

THE PASSING OF THE FRISIANS.

Anthropography of Terpia.
By D. J. H. Nyèssen. Martinus Nijhoff
7.50 guilders 6¼ x 9½; 296 *The Hague*

This book is a study of the early inhabitants of the terps or mounds of the northern coastal region of Holland. A great part of the book is taken up with craniometric investigations, from which the author concludes that the inhabitants of the Friesland terps were racially differentiated from those of the Groningen terps. Whether he is justified in this conclusion we cannot say; because the statistical treatment of the material is grossly defective. His procedure throughout is to compare two distributions, with their means and ranges (and we have not always been able to check his computation of the mean), and to assert that they are different or similar on the basis of inspection. There is nowhere a test of goodness of fit: there is not even a mention of a probable error. And yet we find him saying: "The value of many a protracted inquiry performed in Holland, has been less than might have been expected, on account of an *insufficient knowledge of method, and also of statistics.*" (The author's italics).

We ought, however, to say that he has given the actual frequency distributions, so that anyone who wishes to apply proper statistical methods to the data may do so.

DENTITION AS A MEASURE OF MATURITY. *Harvard Monographs in Education No. 9.*

By Psyche Cattell. Harvard University Press
$1.00 *Cambridge*
6¾ x 10; viii + 91 (paper)

The purpose of this study is to establish standards of physical development on the basis of the state of eruption of the teeth. The subject is briefly reviewed and the standards previously developed criticized. The authoress proposes as a result of her own investigations, standards that depend on the total number of teeth present rather than a method of weighting by the particular type of teeth or the degree of eruption. There is a consideration of sex and race differences, and finally it is advocated that the dental standards be combined with others, such as those based on anatomical measurements and carpal development, into an index of general physical maturity. We are not impressed with the wisdom of this last suggestion. The correlations between the ages estimated by the different standards are low, indicating, so far as these standards refer at all to physical development, that development in one system does not proceed *pari passu* with that of another. To combine the different measures into a simple index would therefore tend to obscure rather than to increase their utility.

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PREHISTORIC MAN.

By Keith Henderson. *E. P. Dutton and Co.*
$3.00 5½ x 8; xv + 276 *New York*

A popular account of early man, intended for the general reader. It forms one number of the "Simple Guide" series, published in this country by Dutton. It is abundantly, and rather well, illustrated with line drawings by the author. It contains nothing new, and a good deal of the purely speculative generalization in which popular writers on prehistoric man are so inclined to indulge. And how fond such writers are of using nice, juicy words, without stopping to think precisely what they mean. For example Mr. Henderson says on p. 47: "Another male from La Chapelle aux Saints. Here again we get that impression of heavy strength in a body still redolent of the beast." Now to be "redolent" is to be "full of or diffusing a pervasive odor; especially, smelling sweet or agreeable." We doubt that the Chapelle skull exhales any odor of the beast, sweet or otherwise.

THE EMPLOYMENT OF WOMEN AT NIGHT. *Bulletin of the Women's Bureau, No. 64.*

By Mary D. Hopkins.
Government Printing Office
Free *Washington, D. C.*
5¾ x 9; 86 (paper)

This report deals not only with the conditions of night employment in the United States but also with the protective legislation for women in foreign countries. Included in the report is the text of the Bern and Washington conventions. Considerable space is devoted to a discussion of the harmful effect of night work upon the physical condition of laborers, it being generally agreed that it is "disproportionately more harmful to a woman's physique than to a man's." Reading the testimony of various experts who have studied the employment of night labor from a purely economic point of view one is inclined to the view that at least some of the ills of industry would be mitigated if night work were abolished for both sexes.

PRESCRIBING OCCUPATIONAL THERAPY.

By William R. Dunton, Jr.
Charles C. Thomas, Inc.
$2.10 (cloth) *Springfield, Ill.*
$1.35 (paper)

The definition of occupational therapy in the meaning of this little book is "any activity, mental or physical, definitely prescribed and guided for the distinct purpose of contributing to and hastening recovery from disease or injury." The author's experience has apparently been mostly in the field of psychiatry, but he has given much thoughtful attention to the subject in general. There is a short, not very searching discussion of principles, followed by separate chapters on specific applications to mental disorders, general medical, surgical, orthopedic, cardiacs, tuberculous, children, and bed occupations. There is an intelligent recognition that this form of therapy is only ancillary to general medical treatment, and from this view the book ought to be of help to the practicing physician.

THE PEOPLE OF THE TWILIGHT.

By Diamond Jenness. The Macmillan Co.
$3.00 5½ x 8½; 247 *New York*

The author spent two years among the Esquimaux of the Coronation Gulf Region and here recounts his experiences among them. He developed a great attachment for the people and tells of their manners and difficulties with deep sympathy and appreciation. In conclusion he laments the threatened extermination of this picturesque and happy folk by the action of invading traders. For the sake of the furs that may be secured, the natives are supplied with high power guns; by means of these the scant source of meat is soon exhausted, and the people starved to extinction.

The book is provided with an introduction by Fridtjof Nansen, and contains a number of illustrations as well as a map of the region traversed.

HUNGER FIGHTERS.

By Paul de Kruif. Harcourt, Brace and Co.
$3.50 5¾ x 8½; 377 *New York*

Last night the reviewer dined with a number of medical men, who were all of the decided opinion that *Hunger Fighters* was a much better book than *Microbe Hunters*. It seems to us not quite so good as that masterpiece. The reason is that, with a few exceptions—notably Mark Carleton—the men discussed in *Hunger Fighters* seem intrinsically less interesting and less significant men than those in *Microbe Hunters*. But after all, who are we to pass such a judgment? It is enough to say that Paul de Kruif has written another book about another group of biologists which every subscriber to this Review will want to read. There is the same gusto, the same insight, and the same pungent and often subtle commentary on the history of science that made *Microbe Hunters* a great book.

HIDATSA EAGLE TRAPPING. *Anthropological Papers of The American Museum of Natural History. Vol. XXX, Part IV.*

By Gilbert L. Wilson.

The American Museum of Natural History
$1.50 6½ x 9¾; 146 (paper) *New York*

An interesting account of the methods of trapping eagles used by the Hidatsa Indians, in the form of narratives by Wolf-chief, a Hidatsa born about 1849, and recorded in 1915. Eagle trapping was a ceremonial affair, with a complicated ritual; but apparently it was not unknown for somewhat irreverent young men to go out on their own and trap eagles with a minimum of attention to the formal observances officially prescribed. The first of Wolf-chief's narratives tells of such an expedition; the second tells of an eagle trapping expedition on which all the rules were followed. Apparently there was no penalty attached to departures from tradition, nor even any serious objection on the part of the more orthodox members of the tribe.

MAN A MACHINE. *In Answer to a Romantical and Unscientific Treatise Written by Sig. Eugenio Rignano and Entitled "Man Not a Machine."*

By Joseph Needham.
W. W. Norton and Co., Inc.
$1.00 $4\frac{1}{8}$ x $6\frac{1}{2}$; 103 *New York*

A well written little book, which, however, is not quite what the title would lead one to suppose. Most of the book is occupied in a refutation of Rignano's teleological argument for vitalism; but, having demolished Rignano, the author goes on to explain that he does not really mean that man is a machine, but only that unless he is a machine he cannot be treated scientifically, and that therefore science is compelled to assume that he is. But he at once concedes that this is fundamentally a methodological fiction, and admits the right of philosophers and theologians to consider man as anything else they like. The concession seems fair to us, but we understand that it rather galls Mr. Mencken.

A CENSUS OF EPILEPTICS KNOWN TO THE PUBLIC AUTHORITIES IN THE COUNTY OF SURREY.

Permanent Committee on Epileptics
London
$8\frac{1}{4}$ x $13\frac{3}{4}$; 19 (mimeographed)

Figures as to the incidence of epilepsy in the general population are practically non-existent. The present paper gives the results of a census of epileptics known to the public authorities in the population of Surrey (including the County Borough of Croydon). The material includes reports on 726 epileptics, and has been tabulated with respect to age, sex, mental conditions, and physical defects. As a result of this investigation, it is estimated that there are something like 25,000 epileptics chargeable to the public authorities in England and Wales.

AN ANALYSIS OF MAGIC AND WITCHCRAFT. *A Retrospective Introduction to the Study of Modern Metapsychics.*

By C. W. Oliver. *Rider and Co.*
15 s. net 6 x 9; xi + 244 *London*

An outline of the various magical beliefs and practices which have existed in historic times, mainly in Western Europe. The book is, according to the author, intended as an introduction to the study of metapsychics or, in more usual terminology, spiritualism; but we should be less than fair if we implied that belief in spooks is prominent in the book. However, we doubt that the book will be found of great value; the same thing has been done before and done better.

RASSENKUNDE DES SCHWEDISCHEN VOLKES.

Edited by H. Lundborg. *Gustav Fischer*
16 marks (paper) *Jena*
19 marks (cloth)
8 x 11; viii + 160 + 50 plates

The English edition of this important contribution to human biology has already been noticed in these pages. While this German edition is somewhat condensed it is not harmfully so. Furthermore it contains some material not in the original English edition. It is a work of first rate importance and enduring value.

CANNIBAL JACK: *A True Autobiography of a White Man in the South Seas.*
By William Diapea (Printed from the manuscript in the possession of the Rev. James Hadfield, with a foreword by H. de Vere Stacpoole). *Faber and Gwyer, Ltd.*
7 s. 6 d. net *London*
$5\frac{1}{8}$ x 8; xxii + 242

We are not going to commit ourselves as to the veracity of this narrative. It purports to be a fragment of the autobiography of a South Sea trader, covering a period in the eighteen-forties. There is a glowing preface by H. de Vere Stacpoole, who rates the book with *Omoo* and *Typee*, which is a matter of opinion. Frankly, we did not get much of a kick out of the book.

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OBSERVATIONS ON HUMAN HEREDITY.
By J. S. Manson. *H. K. Lewis and Co., Ltd.*
6 s. net *London*
$5\frac{3}{8}$ x $8\frac{1}{2}$; ix + 84

The greater part of this book is taken up with pedigrees of various abnormalities. The most valuable, because most complete, are those on hereditary lamellar cataract and on hereditary syndactylism and polydactylism.

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THE BANTU TRIBES OF SOUTH AFRICA. *Reproductions of Photographic Studies. Vol. I, Section I, Plates I–XX. The Bavenda.*
By A. M. Duggan-Cronin (with an introductory article on the Bavenda and descriptive notes on the plates by G. P. Lestrade).
Deighton, Bell and Co., Ltd.
Cambridge
15 shillings (postage 6 pence)
$8\frac{1}{8}$ x $11\frac{1}{2}$; 23 + 20 plates (paper)

A short description of the Bavenda, and twenty excellent reproductions of photographs. When completed this will be an extremely valuable anthropological reference work.

* * *

PREHISTORIC MAN. *Reading with a Purpose (No. 43).*
By George G. MacCurdy.
American Library Association
Cloth, single copy, 50 cents *Chicago*
10 or more copies, 45 cents each
Paper, single copy, 35 cents
4 copies, $1.00
10 copies, $2.25
25 copies, $4.50
50 copies, $6.50
100 or more copies, 11 cents each
$4\frac{3}{4}$ x $6\frac{7}{8}$; 45

A very brief sketch of prehistory, with a useful short selection of books for the general reader.

* * *

ZOOLOGY

THE BRITISH SEA ANEMONES.
By T. A. Stephenson. Printed for the Ray Society. Sold by Dulau and Co.
£1:17:6 *London*
$5\frac{1}{2}$ x $8\frac{5}{8}$; xiv + 148 + 14 plates

"The material presented here has been derived partly from a personal investigation of Actinian anatomy extending over a number of years, and dealing with species from many parts of the world as well as with those of the British area. This has been supplemented by an extensive study of living material, including not only attention to the external form of the living animal, but also an investigation of the methods of reproduction prevalent within the group, together with general observation of natural history." The descriptions have been written direct from living animals, with the aid of a binocular dissecting microscope, and the notes on the range of variation given under each species are based largely upon personal experience. The book deals with the sub-order Actiniaria only, and does not include the Ceriantharia and Zoanthinaria.

It might be misunderstood from the title that the book is mainly taxonomic; more than half is devoted to a general account under the headings of structure, coloration, development, bionomics, and classification. Following are a list of British Actinaria, a list of the literature and an index of technical terms. The book is generously illustrated and contains a number of beautiful colored plates. We are delighted with Neptune's daughter as figured in the end pieces.

FIELD BOOK OF NORTH AMERICAN MAMMALS.

Descriptions of every mammal known north of the Rio Grande, together with brief accounts of habits, geographical ranges, etc.

By H. E. Anthony. *G. P. Putnam's Sons*
$3.50 3⅞ x 6¾; xxv + 625 *New York*

In this book are collected, in condensed form, all of the important faunistic data concerning North American mammals, both land and marine. For each large group of mammals there is a full and detailed description with brief synopses of the other related forms. The 32 colored plates and 200 other illustrations are well chosen as an aid for studying the different types.

With this manual at hand the layman will have little difficulty in identifying most of the species and subspecies of mammals which he meets anywhere in North America north of the Rio Grande. The descriptions, common names, ranges, etc. are in terms which he can easily comprehend. Even the specialist on mammals will find this a useful book to have at hand. There are indices of both Latin and common names, a lengthy bibliography and distribution maps.

THE ECOLOGY OF AN HAWAIIAN CORAL REEF.

Bernice P. Bishop Museum Bulletin 45.
By Charles H. Edmondson. *The Museum*
$1.00 6⅞ x 10; 64 (paper) *Honolulu*

The report of an intensive ecological study of a section of Waikiki reef. In addition to the field work experimental work was carried on on twenty-three forms of corals inhabiting this section. The principal point of attack was the problem of the responses of the coral animals to various environmental factors, notably temperature, salinity, silt, sunlight, etc. The range of variation in conditions which the animals are able to survive is not so wide as might have been expected *a priori*, save in the case of salinity of the water, where there is an extensive range of adaptability. Altogether this is a thorough and interesting piece of research.

BIBLIOGRAPHY OF SPONGES, 1551–1913.

By G. C. J. Vosmaer. Edited by G. P. Bidder and C. S. Vosmaer-Röell.
The Macmillan Co.
$5.25 5⅜ x 8⅝; xii + 234 *New York*

This extensive bibliography which was begun in 1880, was unfinished at the time of the author's death in 1916. The manuscript has been completed and edited by Madame Vosmaer and Dr. G. P. Bidder.

The list of titles, the earliest of which is a work by Entzel, appearing in 1551, and the most recent by Zahalka, published in 1913, includes books and articles on recent as well as fossil sponges. Abstracts, translations, reviews, etc., with a few exceptions, have been excluded from the list. The bibliography is preceded by the author's preface as well as one by Dr. Bidder and is concluded by an index of the names of the authors given in the list. It is a valuable reference work for all those interested in sponges.

AFRICAN JUNGLE LIFE.

By A. Radclyffe Dugmore.

The Macmillan Co.
$6.00 7¼ x 10; viii + 246 *New York*

In recent years a number of books have appeared on animal life in the jungle in which the authors have more or less abandoned the method of describing their observations in a purely objective manner and have sought to convey to the reader an understanding of what existence for some of the "big game" animals really means from the animal view point. Such books are interesting when done by persons who have had long acquaintance with jungle animals. The present volume qualifies as one of the finest examples of its kind. The author, without obvious exaggeration, describes the pleasures and worries, the affections and fears, and the struggles to live of five types of animals—the elephant, the lion, the buffalo, the rhinoceros and the giraffe. The book is beautifully illustrated.

THE LEAFHOPPERS OF OHIO. *Ohio Biological Survey Bulletin 14 (Vol. III, No. 4).*

By Herbert Osborn. *University Press*
$1.00 *Columbus, O.*
6¾ x 9¾; 175 (paper)

Represents records accumulated for 30 years on the Cicadellidae of the State of Ohio, and includes some of the species which have not as yet been collected within the borders of the state, but which from their occurrence in adjacent states and in some cases from the Atlantic coast to the Mississippi River will no doubt be found when sought under the proper conditions. "The paper will therefore serve as a fairly complete survey for the group for the Ohio River valley or the territory from the Alleghenies to the Mississippi River and from Lake Erie to Tennessee."

There is an index to the genera and a short list of references.

EXPERIMENTAL STUDY OF THE FUNCTION OF THE OYSTER GILLS AND ITS BEARING ON THE PROBLEMS OF OYSTER CULTURE AND SANITARY CONTROL OF THE OYSTER INDUSTRY. *Bureau of Fisheries Document No. 1035.*

By Paul S. Galstoff.

Government Printing Office
15 cents *Washington, D. C.*
7½ x 11; 39 (paper)

The author's investigations deal with the rate of flow produced by the oyster gills, with special reference to the effects of temperature; with the filtering action of the gills; and with the length of time the oyster shell is open. He finds that no current is produced at 5°C., and that the optimum temperature is between 25° and 30°. The gills filter out from 80 to 99 per cent of the plankton organisms. The average period during which the oyster shell was open was 17 hours out of 24, with no correlation with the time of day.

IV. TERTIARY AND PLEISTOCENE MOLLUSCA FROM THE GALAPAGOS ISLANDS. V. LANDSHELLS OF THE GALAPAGOS ISLANDS.

Proceedings of the California Academy of Sciences. Fourth Series. Vol. XVII, Nos. 4 and 5.
By William H. Dall and Washington H. Ochsner. *California Academy of Sciences*
75 cents *San Francisco*
7⅜ x 10; 96 + 8 plates (paper)

Both of the authors of this report are deceased. The contents are an edited presentation of an almost complete manuscript left by them, giving their findings during the 1905–1906 expedition from the California Academy of Sciences to the Galapagos Islands. Part IV deals with fossil Mollusca. Part V gives an introduction to geographical and meteorological conditions of the Islands, and an account of the landshells. There are a considerable number of photographic illustrations.

DIPTERA BRACHYCERA AND ATHERICERA OF THE FIJI ISLANDS.

Based on Material in the British Museum (Natural History).
By Mario Bezzi.
British Museum (Natural History)
5½ x 8½; viii + 220 *London*

The author of this volume, whose death occurred before its publication, found the dipterous fauna of Fiji to be "a typically endemic one of Austro-Malayan origin, with a small number of imported elements." From specimens forwarded to him by a number of collectors of Diptera of the Fiji Islands he was able to increase the number of species from the thirty already recorded to two hundred and thirty-nine. In the text of this volume are 54 figures. There is an index of families, genera and species.

THE MOSQUITOES OF THE AMERICAS.

Carnegie Institution of Washington Publication No. 387.
By Harrison G. Dyar.
Carnegie Institution of Washington
$6.00 (cloth) *Washington, D. C.*
$5.00 (paper)
6¾ x 10; 616

A detailed and exhaustive presentation of the taxonomy of the sub-family Culicinae of the family Culicidae of the order Diptera, as found in the Americas.

We note with regret the report of the recent death of the author at the age of 62. He was one of the foremost authorities on mosquitoes in our country.

FOOD OF BULLHEADS.

Bureau of Fisheries Document No. 1037.
By Louella E. Cable.
Government Printing Office
5 cents *Washington, D. C.*
5⅞ x 9⅛; 15 (paper)

The chief findings of this study are the following:

> Bullheads prefer animal food in the form of insect larvae, pupae, and nymphs, crustaceans, bivalve mollusks, and snails, but are able to take other food in the absence of these.
>
> Bullheads do not eat the eggs nor the young of other fish, except occasionally in very small amounts.
>
> Juvenile bullheads eat virtually the same kinds of food as adults.

PHYSIOLOGUS. *A Metrical Bestiary of Twelve Chapters.*

By Bishop Theobald (Translated by Alan W. Rendell). John and Edward Bumpus, Ltd.
10 s. 6 d. *London*
5½ x 8⅛; xxvi + 100

This is a beautifully printed new translation of Bishop Theobald's pious verses about animals. The text of the original edition is reproduced in facsimile. The translation is charming, and the very full commentaries and annotations furnish the background necessary to a complete appreciation of a noteworthy addition to the library of any biologist with antiquarian or theological tastes.

EINFÜHRUNG IN DIE TIERKUNDE.

By Albert Fleischmann *Gustav Fischer*
10.50 marks (paper) *Jena*
12 marks (cloth)
6⅞ x 10¼; viii + 228

This textbook is designed to cover the first semester's work in general zoology. It follows conventional lines, but commendably works in more embryology than corresponding American courses usually do. American teachers will get some pedagogical hints by looking it over. It is well illustrated and indexed.

A LABORATORY MANUAL OF INVERTEBRATE ZOOLOGY.

Fourth Edition, Revised.
By Gilman A. Drew. With the aid of former and present members of the Zoological staff of instructors at the Marine Biological Laboratory, Woods Hole, Mass. W. B. Saunders Co.
$2.25 *Philadelphia*
5 x 7⅝; xiii + 234

A fourth edition of the manual used in courses at the Marine Biological Laboratory at Wood's Hole. It has been revised by the staff of the Laboratory so as to bring the classification, literature lists and nomenclature up to date. Also some of the directions for laboratory class work have been modified.

NORTH AMERICAN FAUNA No. 51. *A Taxonomic Review of the American Long-tailed Shrews (Genera Sorex and Microsorex).*

By Hartley H. T. Jackson.
Government Printing Office
50 cents *Washington, D. C.*
5¾ x 9⅛; 238 (paper)

A thorough and careful revision of the genera *Sorex* and *Microsorex*. The author recognizes 89 forms of 39 species. There are illustrations of skulls and teeth, a bibliography, and an index.

PRAIRIE BIRDS.

By B. J. Hales. *The Macmillan Co.*
$3.00 5 x 7½; xv + 334 *New York*

Descriptions, with some remarks on their habits, of the birds of the Canadian prairies. A useful guide for the amateur.

THE ELASMOBRANCH FISHES.

By J. Frank Daniel.
University of California Press
$5.00 7 x 10¼; xi + 332 *Berkeley*

A second edition, somewhat enlarged by the addition of new material and illustrations, of a standard zoological text.

BOTANY

NORTH AMERICAN ORCHARDS.

Their Crops and Some of Their Problems.
By William H. Chandler. *Lea and Febiger*
$4.50 5¼ x 7¾; 516 *Philadelphia*

A practical book for the orchardist. The author has an extensive acquaintance of the fruit growing industry in widely separated areas. That he sees clearly the problems and difficulties of those who make a business of fruit growing is indicated when he states that "the educated orchardist must base his judgements (diagnoses) in part upon such general scientific principles as we know, but usually in much larger part upon knowledge of many details and unexplained experiences." He points out that very often there must be uncertainty as to what is the best practice in orchard growing in spite of all that science has contributed to a knowledge of it. Not only must the orchardist be acquainted with the problems of climatic response, outstanding diseases, insect enemies, bearing habits and market qualities of the fruit of the varieties that he may grow, but he must likewise know what these problems are for his competitors in other sections of the country.

Notwithstanding the solidly written 500 pages, and the fact that the book is written primarily for the man who operates the orchard for a living, it is in no way formidable. Devoid of technicalities, the amateur will find it not only within his ken but interesting reading as well. At the end of each chapter there are lists of suggested reading for those who wish to study a particular subject more intensively. There is a detailed index.

PRINCIPLES OF PLANT PHYSIOLOGY.

By Oran Raber. *The Macmillan Company*
$3.00 5½ x 8½; 377 *New York*

A new textbook of plant physiology intended, so the author says with emphasis, for *students* and not for *teachers*. The material is well organized and well presented. In fact it is so good that we wish the author would now write an advanced textbook on the same subject. The chief criticism we are inclined to make of the book is that it seems a little out of balance. Out of a total of thirty-one chapters twenty-three deal with one or another aspect of metabolism; one with growth; and two with irritability and movement. Surely these three latter subjects deserve more space, even in an elementary text. We do not urge the cutting of the other parts, but the expansion of these. But, even as it stands, the book is an excellent one.

THE GASTEROMYCETES OF THE EASTERN UNITED STATES AND CANADA.

By William C. Coker and John N. Couch.
The University of North Carolina Press
$12.00 *Chapel Hill*
7¾ x 10¾; ix + 201

A beautifully printed and exhaustive handbook of the Gasteromycetes. For its preparation all the available species were studied at first hand, including those at Persoon's herbarium at Leiden, Bresadola's at Stockholm, Kew Herbarium, New York Botanical Garden Herbarium, Curtis Herbarium, Schweinitz Herbarium, Lloyd Herbarium, and the Pathological and Mycological Herbarium at Washington.

There are a large number of photographic plates, extensive bibliographical references, and an index. The University of North Carolina is to be congratulated on this splendid production.

A LABORATORY MANUAL OF GENERAL BOTANY.

By Emma L. Fisk and Ruth M. Addoms.

The Macmillan Co.

$1.00 5½ x 8½; ix + 103 *New York*

These exercises have been written "to accompany the Revised Edition of 'A Textbook of General Botany' by Smith, Overton, Gilbert, Denniston, Bryan and Allen, and in general a similar order of treatment has been observed." "The general plan of the course is to introduce the subject through a study of seed plants, and to use the facts and principles learned as a basis for a comparative study of the main groups of the plant Kingdom." The directions are clearly and simply presented, and there is a sufficient amount of brief explanatory text to make the immediate objectives intelligible without reference to outside sources.

FACTORS IN THE INCEPTION AND DEVELOPMENT OF FUSARIUM ROT IN STORED POTATOES. *United States Department of Agriculture Technical Bulletin No. 62.*

By Freeman Weiss, J. I. Lauritzen and Philip Brierley. *Government Printing Office*

15 cents. *Washington, D. C.*

5¾ x 9; 36 (paper)

Fusarium rot is responsible for a loss of from 5 to 10 per cent of the annual potato crop of the country. The present bulletin gives an account of experimental investigations of various factors of importance in the development of the rot, especially temperature, humidity, injury to the tuber, and differences in varieties of potato. Recommendations are given as to the treatment of potatoes to minimize loss from rot.

A TEXTBOOK OF GENERAL BOTANY.

By Gilbert M. Smith, James B. Overton, Edward M. Gilbert, Rollin H. Denniston, George S. Bryan and Charles E. Allen.

The Macmillan Co.

$3.75 5⅝ x 8½; x + 539 *New York*

A revised edition of this excellent text. The same plan and order of presentation as that of the original work is preserved here, but there has been a good deal of expansion in the treatment. Chapter XXXII on Evolution might better have been placed last, where it could be easily removed for an edition to be distributed in those states of our Bible Belt where biology is still studied.

PRINCIPLES OF PLANT PATHOLOGY.

By Charles E. Owens.

John Wiley and Sons, Inc.

$4.75 6 x 9; xii + 629 *New York*

An excellent general textbook of plant pathology for students in agricultural colleges. Part I deals with general topics, while Part II discusses in detail particular diseases, classified on an etiological basis. The book is thoroughly illustrated, documented, and indexed, and should take rank as a standard text in its field.

FIELD MANUAL OF THE FLORA OF OHIO AND ADJACENT TERRITORY.

By John H. Schaffner. *R. G. Adams and Co.*
$3.00 4½ x 6¾; 638 *Columbus, O.*

A pocket manual by means of which plants of Ohio and the adjacent territory can be identified from fresh material. In general the characters used are the flowers and vegetative parts present when the plant is in bloom. There is a glossary of common botanical terms and an index.

POLLENANALYTISCHE UNTERSUCHUNGEN AN SCHWEIZER-MOOREN UND IHRE FLORENGESCHICHTLICHE DEUTUNG. *Veröffentlichungen des Geobotanischen Institutes Rübel in Zürich. 5. Heft.*

By Paul Keller. *Hans Huber*
6⅜ x 9¼; 163 (paper) *Bern*

Detailed results of an investigation of the stratigraphy of Swiss peat bogs, carried out by an ingenious method, which depends upon the identification in the borings of the pollens of some ten species of forest trees.

MORPHOLOGY

THE DEVELOPMENT OF THE HUMAN EYE.

By Ida C. Mann. *The Macmillan Co.*
$12.00 6¼ x 9¾; x + 306 *New York*

Certainly the most authoritative and comprehensive treatise in English on the embryology of the eye. Based on profound knowledge and extensive original research with an exceptionally complete series of human embryos, lucidly written, simply but clearly and profusely illustrated by the author, it is a work deserving of high praise. Both the general biologist interested in the subject as an aspect of ontogeny, and the ophthalmologist concerned with the origin of congenital eye defects will turn to it for reference.

A LABORATORY MANUAL FOR COMPARATIVE ANATOMY.

By Malcolm E. Little and Rudolf T. Kempton.
The Macmillan Co.
$2.25 5½ x 8½; xix + 286 *New York*

A new laboratory guide in vertebrate comparative anatomy, planned to steer a compromise course between the Huxleyan method of studying types exclusively, and the more recent pedagogic technique of focussing attention upon organ systems. The material is well arranged for teaching purposes.

PHYSIOLOGY AND PATHOLOGY

LABORATORY DIAGNOSIS AND EXPERIMENTAL METHODS IN TUBERCULOSIS.

By Henry S. Willis (With a Chapter on Tuberculo-Complement Fixation, by J. Stanley Woolley, and Introduction by Allen K. Krause).
Cloth: $3.50 *Charles C. Thomas*
Keratol: $4.25 *Springfield, Ill.*
6 x 8¾; xxv + 330

The multifarious aspects of tuberculosis have assumed such large dimensions and become so complicated with detail that it requires expert and long study to become thoroughly acquainted with even individual phases. The author of this volume is eminently qualified in this respect to deal with the subject in hand. He has for many years been associated with the Kenneth Dows Research Laboratories for the study of tuberculosis at the Johns

Hopkins Hospital, and has had opportunity to deal critically and at first hand with all the laboratory methods that pertain to the study and treatment of tuberculosis.

The work comprises five parts: I. General considerations of the body fluids and excreta; II. Bacteriological diagnosis; III. Diagnosis by use of tuberculin; IV. Serological diagnosis; V. Some methods of value in studies of tuberculosis experimentally produced. It is clearly written, with many illustrations, provided with detailed practical directions, a long bibliography, and an index. The book should be in every laboratory concerned in any way with tuberculosis, and consulted by every student who expects to meet the disease as a practical problem.

THE RESPIRATORY FUNCTION OF THE BLOOD. *Part II: Hæmoglobin.*

By Joseph Barcroft. *The Macmillan Co.*
$5.00 6⅝ x 9¾; ix + 200 *New York*

The classical studies of Barcroft recorded in his *Respiratory Functions of the Blood*, printed in 1913, are to be reissued and brought up to date in a series of separate volumes dealing with different phases of the subject. The first volume, *Lessons from High Altitudes*, appeared in 1925. This is the second and deals with what L. J. Henderson has characterized as the second most interesting substance in the world, hæmoglobin.

In it Barcroft takes up the chemistry of hæmoglobin and its constituent elements, its distribution among species, the statics and dynamics of its combination with oxygen and other gases, its solution properties, and the effect of temperature on it. There is a closing discussion of the biological significance of the substance.

The book is, as is to be expected, well written, in intimate contact with the history of the subject and the personalities who contributed to its development.

There is an index and references are appended to each separate chapter, but there is no general bibliography.

DIE PHYSIOLOGIE DER THYMUS.

By Frederick S. Hammett.
Urban und Schwarzenberg
2.50 marks *Berlin*
7 x 10; 22 (paper)

This little essay is in the series *Fortschritte der Naturwissenschaftlichen Forschung*, edited by Dr. Emil Abderhalden. The author considers the subject didactically under the following heads: Growth of the Thymus; Autolysis of the Thymus with Age; Factors of Internal Secretion associated with Involution of the Thymus; Feeding and Extirpation Experiments; Physiological Effects of Thymus Extracts; The Function of the Thymus. A good measure of what is presented comes from his own work. He concludes "The function of the thymus is not yet clear."

EXERCITATIO ANATOMICA DE MOTU CORDIS ET SANGUINIS IN ANIMALIBUS.

By William Harvey (With an English Translation and Annotations by Chauncey D. Leake). *Charles C. Thomas*
$3.50 *Springfield, Ill.*
6¼ x 9½; 154

A new translation of the *De Motu Cordis*, with some useful annotations. The volume also contains a facsimile of the 1628 edition, and a chronology of Harvey's life. The translation is good, and will probably be found easier reading than the original English translation of 1653, and certainly easier than Willis's translation of 1847. The publisher has attempted to produce a volume which will be a worthy memorial to the tercentenary of the original publication. There is a good index.

THE BLOOD PLASMA IN HEALTH AND DISEASE.

By J. W. Pickering. *The Macmillan Co.*
$4.25 5½ x 8½; xi + 247 *New York*

Specialization grows apace. A book on blood covers too wide a range. So now we have in this volume an excellent text book devoted to the *plasma* of the blood only. Successive chapters deal with the protein of the plasma; fibrinogen; the inception of clotting; stabilization of plasma; thrombins and antithrombins; fibrin; suppression of coagulability *in vivo*; the blood in anaphylaxis; theories of coagulation; arrest of hemorrhage; thrombosis; menstrual and puerperal blood; and the blood of bleeders. There is a bibliography of some seventeen closely printed pages, and a detailed index. This is a useful addition to the literature.

LABORATORY EXPERIMENTS IN PHYSIOLOGY.

By W. D. Zoethout. *The C. V. Mosby Co.*
$2.25 6 x 9; 251 *St. Louis*

While this laboratory guide was planned to accompany the author's textbook, it is so arranged that any other textbook will serve about as well. As it is intended for the student whose time for the subject is somewhat limited, it is not burdened with unnecessary matter. "Preparation" questions prefacing each experiment are to be studied before going to the laboratory. All kymographic records and coordinate graphs have been omitted, the author considering these to have no place within a laboratory manual.

A TEXTBOOK OF BACTERIOLOGY.

A Treatise on the Application of Bacteriology and Immunology to the Etiology, Diagnosis, Specific Therapy and Prevention of Infectious Diseases for Students and Practitioners of Medicine and Public Health.

By Hans Zinsser (with a section on Pathogenic Protozoa by E. E. Tyzzer).
D. Appleton and Co.
$7.50 6¾ x 9¾; xx + 1053 *New York*

In this sixth edition, the entire contents of the leading American textbook of bacteriology has been revised, bringing all chapters up to date. The original purpose of developing the book into a manual of infectious diseases has been adhered to, so that it still maintains its importance for physicians and health officers, as well as for undergraduate students of medicine.

THÉORIE IONIQUE DE L'EXCITATION DES TISSUS VIVANTS.

By P. Lasareff. *Albert Blanchard*
40 francs 6½ x 10; 240 (paper) *Paris*

An attempt to establish quantitative laws of sensation (taste, smell, etc.), largely through mathematical methods of reasoning and analysis, upon a physicochemical observational base. The book summarizes the results of the work done in the author's laboratory during the past quarter of a century. Dr. Lasareff is Director of the Institute of Physics and Biophysics at Moscow.

CANCER AND CANCER RESEARCH.
A Series of Articles for the Lay Public.
Compiled by a Scientific Committee of the Liverpool Medical Research Organization.
Sherratt and Hughes
1 s. 6 d. *Manchester*
5½ x 8½; 75 (paper)

This is a reprint of a series of articles on various phases of the cancer problem compiled for the lay public by a scientific committee of the Liverpool Medical Research Organization. These appeared first in the Liverpool Daily Post and Mercury for March, April and May, 1928.

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A TEXTBOOK OF PHYSIOLOGY.
By W. D. Zoethout. *The C. V. Mosby Co.*
$4.50 6 x 9; 664 *St. Louis*

The third edition of a book which was especially planned for students in dental, pharmacy and normal schools where the time devoted to physiology is too limited to make advisable the use of any of the larger works as a text. This edition has been throughly revised, many topics added or expanded, while less important subjects have been dropped.

* * *

LEHRBUCH DER PHYSIOLOGISCHEN UND PATHOLOGISCHEN CHEMIE.
In 75 Vorlesungen für Studierende, Ärzte, Biologen und Chemiker. II Band: Stoffwechsellehre. VI (Schluss-) Lieferung: Purin und Kohlehydratstoffwechsel, Vorlesung: LXIII bis LXXV.
By Otto Fürth. *F. C. W. Vogel*
15 marks *Leipzig*
7 x 10; vi + 280 (paper)

This fascicle completes the second volume of this new edition of a standard text, of which earlier parts have been noticed in THE QUARTERLY REVIEW OF BIOLOGY. It deals with purine and carbohydrate metabolism.

* * *

HUMAN PHYSIOLOGY. *A Text-Book for High Schools and Colleges. Fifth Edition Revised.*
By Percy G. Stiles. *W. B. Saunders Co.*
$2.25 5 x 7¾; 444 *Philadelphia*

A fifth edition of Professor Stiles' well known text book. It is well adapted for high schools, but there are some uplifting passages which do not add materially to its value.

* * *

TIERPHYSIOLOGISCHES PRAKTIKUM *für Studierende der Landwirtschaft und Veterinärmedizin.*
By E. Mangold. *Julius Springer*
3 marks 5⅝ x 8¼; 53 (paper) *Berlin*

Laboratory directions for a year's course in animal physiology, with two laboratory periods per week.

BIOCHEMISTRY

THE PROTAMINES AND HISTONES.
By A. Kossel (Translated by W. V. Thorpe).
Longmans, Green and Co.
$3.25 6 x 9½; xi + 107 *New York*

The group of substances comprising the subject matter of this work is of a rather specialized interest, and their study does not come under the purview of the general chemist's work. It is all the more fortunate therefore that the extensive investigation of them by the author was rescued for science before his death, and presented in this easily available form to English readers.

The protamines and histones are proteins characterized by their basic reaction, as distinguished from the acid reaction of the more widely distributed proteins, the protamines being in addition specially noteworthy for their simplicity of structure. Of particular interest to the biologist is their association with the nuclear portion of the cell, and their biological distribution, the protamines being limited to the sperm of certain fish, and the histones to the germ plasm of some vertebrates and invertebrates, the red cells of birds and the thymus gland of certain mammals.

There is a long bibliography and an index.

◆

THE DETERMINATION OF HYDROGEN IONS. *An Elementary Treatise on Electrode, Indicator and Supplementary Methods with an Indexed Bibliography on Applications.*

By W. Mansfield Clark.

The Williams & Wilkins Co.
$6.50 6 x 9; xvi + 717 *Baltimore*

The third edition of this standard treatise has been greatly, indeed almost completely, rewritten. The total pages have increased from 480 to 717 (49 per cent increase); the subject index covers 51 per cent more space, and the author index covers 154 per cent more space. The bibliography on applications has been completely revised, and now consists of some 1600 titles, of which only about 600 were included in the second edition.

Those interested in growth curves may well glance at the diagram on page x, showing the number of papers dealing with pH measurements published each year from 1911 to 1927; in the latter year the total was over 1450.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 272.*

Containing following articles: *Methodik der Gewebselastometrie und der H-Ionenmessung am lebenden Organismus*, by Heinrich Schade and Karl Mayr; *Die polarographische Methode*, by Silvester Prát; *Die Pufferlösungen bei der colorimetrischen Bestimmung der Wasserstoffionen-konzentration*, by I. M. Kolthoff; *Methodik der Bestimmung der Capillarität*, by Karl Schultze.

Urban und Schwarzenberg
9 marks 7 x 10; 172 (paper) *Berlin*

Lieferung 283. Containing following articles: *Die quantitative Spektralanalyse*, by M. C. Keller; *Die Verwendung des Schmalfilms für biologische Zwecke*, by W. R. Hess; *Farbmessungen an gefärbten Körperflüssigkeiten mit dem Pulfrichschen Stufenphotometer*, by Ludwig Heilmeyer.

Urban und Schwarzenberg
6 marks 7 x 10; 104 (paper) *Berlin*

Lieferung 284. Photographische Absorptionsspektrophotometrie.

By Günther Scheibe.

Urban und Schwarzenberg
3 marks 7 x 10; 50 (paper) *Berlin*

These three numbers in the great Abderhalden handbook are of primary interest to biochemists and biophysicists. They impress one once more with the thoroughness and comprehensiveness of this colossal undertaking.

◆

DIE METHODIK DER FERMENTE. *Lieferungen II und III.*

Edited by Carl Oppenheimer and Ludwig Pincussen.

Georg Thieme
Leipzig
Lief. II, 28 marks
7¾ x 10½; vii + 304 (paper)
Lief. III, 28 marks 944 (paper)

Part I of this work, which is projected

as a comprehensive treatise on ferments, was noted in this Review (Vol. III, No. 3, 452–3). Parts II and III follow the general arrangement there described, i.e., various general divisions of the subject are taken up independently by different authors. Part II continues the consideration of substrates begun in I and contains a division *C* devoted to the obtaining and purification of ferments. Part III begins the second main division, which includes chapters on the esterases, diastases, nucleoses, urease, and arginase.

COLLOID CHEMISTRY.

By The Svedberg in collaboration with Arne Tiselius. *Chemical Catalog Co., Inc.*
$5.50 5¾ x 9; 302 *New York*

The second edition of a standard introductory treatise to the subject of the physics and chemistry of colloids. The work has been thoroughly revised and enlarged in this edition, more attention in particular being paid to X-ray analysis of the structure of sols and gels, Donnan potentials, the technique of ultramicroscopy, and the measurement of diffusion and cataphoresis.

RECENT ADVANCES IN CHEMISTRY IN RELATION TO MEDICAL PRACTICE.

By W. McKim Marriott.
The C. V. Mosby Co.
$2.50 6 x 9; 141 *St. Louis*

A series of six lectures before the San Diego Academy of Medicine in 1927. The subjects were: fundamental chemical considerations; acidosis and alkalosis; chemistry of the blood; food and metabolism; and endocrines.

APPLIED BIOCHEMISTRY.

By Withrow Morse. Revised and reset with the coöperation of Joseph M. Looney.
W. B. Saunders Co.
$7.00 5¾ x 9¼; 988 *Philadelphia*

The first edition was noticed in The Quarterly Review of Biology, Vol. 1, No. 3. There is nothing to add to what was there said, except that the subject is again brought up to date, eighteen months having elapsed between the writing of the first and second editions.

SEX

THE CONQUEST OF LIFE.

By Serge Voronoff (Translated by G. Gibier Rambaud). *Brentano's*
$3.50 5½ x 8⅛; 201 *New York*

This is a translation of Dr. Voronoff's *La Conquête de la Vie*, which was reviewed here in September, 1928. There is little to add to what was then said. We feel obliged, however, to call attention to this passage: "Abélard, the brilliant poet, never wrote a line after he was emasculated, by the orders of the cruel uncle of Héloïse, at the age of forty." The French text shows that "line" here means "line of poetry"; but whether the fact is an indication of Abélard's diminished intellectual powers (as the author implies) seems doubtful. In point of fact, Abélard wrote a good deal after his operation, but it was theology and not love poetry.

SOME MORE MEDICAL VIEWS OF BIRTH CONTROL.

Edited by Norman Haire.
E. P. Dutton and Co., Inc.
$2.50 5 x 7⅝; x + 216 *New York*

The purpose of this treatise is frankly

propagandist. It is a collection of eleven essays dedicated to Margaret Sanger. All discussion of contraceptive technique is omitted in deference to American laws. We wish that Professor F. A. E. Crew had not lent his name and his pen to this book. To be sure his essay is the best in the lot, as would be expected. But his remarkable talents both as writer and as investigator surely deserve to be put to better uses than bolstering up the respectability of a book like this.

BIOMETRY

F. Y. EDGEWORTH'S CONTRIBUTIONS TO MATHEMATICAL STATISTICS.

By A. L. Bowley. Royal Statistical Society
5 shillings *London*
5½ x 8½; vii + 139 (paper)

Professor Bowley has rendered an important service to mathematical statisticians in this monograph. He has collected and rewritten all of Edgeworth's most important work in statistical theory—no light task. Edgeworth's own papers are by no means easy reading, and not the least of Professor Bowley's services has been to clarify and amplify points which the original papers left obscure.

Whether Edgeworth's work is of great value to the practical statistician seems to us rather doubtful; but we can recommend it to the statistician who is interested in the mathematical philosophy behind his work—not because he ought to agree with all of it, but because it is worth thinking about.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 265.*

Containing the following articles: *Die Methodik biometrischer Messungen an Laboratoriumsversuchstieren*, by Karl Saller; *Rassenpathologische Methoden*, by Albert Plehn; *Zur Technik der Injektion der Lymphgefässe*, by Hermann Baum.

Urban und Schwarzenberg
9 marks 7 x 10; 182 (paper) *Berlin*

The bulk of this number of the Abderhalden handbook is devoted to an extremely valuable discussion of the application of modern, refined, anthropometric and osteometric technique to the smaller laboratory mammals. It is a welcome addition to the literature.

PSYCHOLOGY AND BEHAVIOR

EXPLORING YOUR MIND *with the Psychologists.*

By Albert E. Wiggam. The Bobbs-Merrill Co.
$3.50 5¾ x 8¾; 419 *Indianapolis*

Mr. Wiggam has taken on himself the Huxleyan task of bringing scientists and their works to the layman. Some of the eminent figures of the laboratories who have been thus prominently exposed to the public eye are pleased with the results, others not. We are under the general impression that the "nays" have it.

Hitherto our author has been mostly occupied with genetics and eugenics, and biologists have come in for most of his notice. He now turns his active pen on the psychologists. Having interviewed a number of them, he reports here his impression of their teachings, as gleaned from conversation. The following are represented, *in person* by good portraits, and by excerpts from their remarks: Professor Edward Lee Thorndike, Dr. Donald A. Laird, Prof. Henry Foster Adams, Dr. David Mitchell, Prof. Lewis Madison Terman, Dr. Catherine Cox Miles, Prof. Carl Emil Seashore, Dr. J. McKeen Cattell, Dr. Mark A. May, Dr. Hugh Hartshorne, Dr. Michael I. Pupin.

What Mr. Wiggam understands of the purpose of science may be gathered from two quotations taken from either end of his work.

> In fact, I do not think it does people very much good to learn the marvels of the atom or the germ-cell unless at the same time they are taught how to make this knowledge helpful for solving their daily problems, inspiring for their hours of meditation, consoling in their days of grief, enlightening in their periods of doubt, heartening in their moments of fear, exalting in their times of triumph and success.

And in the *finale* by Michael Pupin, (the eminent electrician somehow gets into this group of psychologists):

> Science is making us better Christians.
>
> Science is teaching men how to cooperate intelligently with God; it is teaching men what His laws are and how to obey them.
>
> Science is proving that the human soul is the greatest thing in the Universe, the supreme purpose of the Creator.
>
> Science is leading us closer and closer to God.

We might be moved to enter a vigorous protest against the intrusion of this sort of evangelism into scientific discussion, but we cannot when Mr. Wiggam is concerned. He writes too entertainingly and good naturedly to bear earnest opposition. He is very effective with the public, and his intentions are the best. Futhermore he is the sort that would be bound to be improving the world one way or another. If science didn't seduce him some other enthusiasm would—and we can think of worse.

THE SYMBOLIC PROCESS AND ITS INTEGRATION IN CHILDREN. *A Study in Social Psychology.*

By John F. Markey. Harcourt, Brace and Co.
\$3.50 $5\frac{1}{2}$ x $8\frac{1}{2}$; xii + 192 *New York*

This book is an attempt to explain the nature and development of language in the child. The author emphasizes particularly the importance of the social processes in the development of the "symbolic process" (which we take to be a high-toned name for language). With some of his statistical analysis we find it hard to agree; we doubt, for example, that he could give any justification for his calculation of a correlation coefficient on page 58. What he has actually done is calculate the correlation between the mean y in an array and the corresponding x for the array; which not unnaturally (since the arrays contain 100 individuals each) gives him a correlation coefficient of $-.975$. Actually, of course, the coefficient will be much less than this, but as we are given no information about the scatter in the arrays it is impossible to say what its value would be.

The book is exceedingly difficult reading. We recommend to Dr. Markey that he meditate upon the literary style of Bertrand Russell, who somehow manages to make subjects of far greater intrinsic difficulty seem much simpler than anything in the present volume.

JUDGMENT AND REASONING IN THE CHILD.

By Jean Piaget (In collaboration with Mlles. E. Cartalis, S. Escher, A. Hanhart, L. Hahnloser, O. Matthes, S. Perret and M. Roud). Harcourt, Brace and Co.
\$3.75 $5\frac{5}{8}$ x $7\frac{1}{2}$; viii + 260 *New York*

Piaget is still a young man, but he has already achieved two notable essays on the psychology of childhood. In *Language and Thought in the Child* he advanced the thesis that thought in the early years is essentially egocentric, i.e., its aim is self satisfaction, and it has not yet felt the obligation to be acceptable to others. In this volume he traces its growth through the ages 11–12 years.

The key to his theory is that the development of thought takes place in the direction of a greater sense of its social responsibility. Logicality arises from the need to have our thoughts carry conviction with others; in the child up to 7–8 years, when ego-centrism is dominant, this quality is absent. Instead it has "juxtaposition" and "syncretism." Juxtaposition is the tendency to juxtapose objects seen together, with no sense of their relation to a synthetic whole, as when a child draws a bicycle by inserting all the parts but not in any functional relation, one to the other. Syncretism is the complementary tendency of seeing the whole in an undifferentiated fusion with no recognition of the relation to it of the constituent elements. After 7–8 years there is a diminution of egocentrism and with this, hand in hand, a development of logicality. The child is able to achieve, though only in a limited way at first, the viewpoint of other individuals, his friends; but not yet the objective outlook that comes with placing oneself in the disposition of inanimate objects. Syncretism, juxtaposition, inability to handle relationships, etc., are still discernable in his thought, but they are shifted to the language plane; in the sphere of action there has been progress from these characters. Accordingly thought characteristically reverts to experience; where hypothetical questions are involved, the child's mind at this stage fails. It is not till 11–12 years that the mind becomes sufficiently liberal in a willingness to separate itself from the ego, to attain the viewpoint of abstract relationship, and the formal reasoning of the adult begins.

So much for the theory in rather inadequate general outline. In support of it the author elicits his analysis of experiments with the use by children of conjunctions expressing causal, logical and discordant relations, their response to the Binet Simon tests by absurd phrases, as well as the logical content of their spontaneous conversation. The experience dealt with is admittedly not large but in good accord with the author's general thesis. The obvious objection to results obtained from an examination of verbal characters, that they may be reflective of the accretion of information and the development of language rather than a change in the character of thought, the author fully appreciates. As regards the possession of requisite information, the simplicity and familiarity of the matters referred to in the tests is appealed to and as respects the acquisition of language, the author holds that the ability to express ideas is precisely the development which marks progress in logical thought.

The study will undoubtedly be welcomed as a support to the school of psychologists who hold to the instrumental, social function of thought, as represented in this country by John Dewey, particularly in his *Experimental Logic*. Like all psychological tracts which it is our fortune to encounter, it seems excessively verbose, and the shuttle movement of the argument, with repeated recourse to points already established makes it heavy reading. It is, however, well translated. There is an index, which helped us not at all to locate several items contained repeatedly in the text.

THE MODERN CAT: HER MIND AND MANNERS. *An Introduction to Comparative Psychology.*

By Georgina S. Gates. *The Macmillan Co.*
$2.00 $5\frac{1}{4} \times 7\frac{1}{8}$; xi + 196 *New York*

In this entertaining book the author, an assistant professor of psychology of Barnard College, discusses in simple and non-technical language what is known of the mind of the greatest of all household pets. The book is mainly a compilation of well known data, written for two classes of readers: "those who love cats and would like to know more about the explanation for their actions, and those who may wish to obtain, through a description of methods employed with one animal, a first glimpse of the ways of comparative psychology."

Many popular beliefs concerning cat behavior are shattered. Much interesting and sound information is given which makes the cat appear to the average reader in a wholly new light. According to the author the cat, while possessing color vision, perceives only shades of gray. "She lives in a visual world much like ours at twilight," also "in an auditory world like that of the tone-deaf individual." Feeding experiments seemed to indicate that there was complete understanding between the cat and the experimenter when with a clapping of hands the words "I must feed those cats" were uttered and food was to be secured for the searching. However, the words "My name is Thorndike" were just as magical in stimulating the cat to search for its food, if uttered a sufficient number of times under the right conditions.

The title of the book is misleading in that there is the suggestion that the cat of today is somehow different from the cat of the past. There are four illustrations and several diagrams showing time curves in trial experiments for both cats and students. A list of the chief references consulted in preparing the book is given, and there is an index.

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THE FUNDAMENTALS OF HUMAN MOTIVATION.

By Leonard T. Troland.

C. Van Nostrand Co.

$5.00 5½ x 8½; xiv + 521 *New York*

Hedonism translated into psychophysical terms. Nociceptive afferent nerve currents—those indicating injurious conditions—are accompanied by a decrease in conductance of the cortical adjustors and consequently by a change in the motor response; beneceptive currents—those indicating favorable conditions—are accompanied by an increase in conductance and a consequent enhancing of the motor response. Troland calls this change of conductance retroflex action, and bridges the psychophysical gap by the postulate that the affective intensity is proportional to the rate of change of conductance. On the basis of these principles he discusses, among other things, the pleasures of novelty, "the nature and foundations of emotional experience, the explanation of typical modern interests: automobiles, radio, and the like," and finally, "suggestions towards a scientific treatment of the problems of ethics." The book is well documented and contains a glossary and an index.

* * *

POLITICAL BEHAVIOR. *The Heretofore Unwritten Laws, Customs and Principles of Politics as Practiced in the United States.*

By Frank R. Kent. William Morrow and Co.

$2.50 5 x 7½; ix + 342 *New York*

All students of human biology should read this entertaining treatise by the leading political writer for the newspapers of these times and parts. It is replete with sound political information as well as realistic philosophy. It is not a book for old ladies of either sex. In fact Mr. Kent says that he

> is fully aware that some of the views herein expressed will likely be resented by those who have, in the words of the politicians of every generation, "an abiding faith in the fundamental intelligence of the American people." The natural tendency of these will be to insist that the opinions here given are warped or soured; that actually the caliber and character of the voters is not as depressingly low as here depicted; that a "broad view" will prove the people to have a real capacity for getting at the truth; that

in the "long run" they can be depended upon to act wisely and righteously. The answer is that it would be pleasant to think so, that perhaps it is a good thing to keep up the pretense, that there is of course a small minority of whom it is so. But so far as the vast majority is concerned the evidence is overwhelmingly against it and every clear-headed person who knows from personal contact the types composing the great bulk of the voters, knows it is not so of them.

HUMAN BEHAVIOR.

By Walter S. Hunter.
The University of Chicago Press
\$2.00 $5\frac{1}{4}$ x $8\frac{1}{4}$; 355 *Chicago*

FUNDAMENTALS OF OBJECTIVE PSYCHOLOGY.

By John F. Dashiell. Houghton Mifflin Co.
\$3.00 $5\frac{5}{8}$ x 8; xviii + 588 *Boston*

These two text books cover practically identical ground, though the arrangement is somewhat different. On the whole we prefer Dr. Hunter's, as being shorter, somewhat better arranged, and rather more attractively printed (though neither stands out as a piece of book-making). Both books take an extreme behaviorist position, though Dashiell is broad-minded enough to admit in his preface that an introspective approach has occasional value.

It is interesting to note that both authors reproduce a part of Goddard's pedigree of the Kallikak family, and express no dissent from his view that feeble-mindedness is a Mendelian recessive.

PSYCHOLOGIE DES ANIMAUX.

By F. Buytendijk (French translation by H. R. Bredo). Payot
25 francs $5\frac{1}{2}$ x 9; 315 (paper) *Paris*

An excellent review, interestingly written, of the present state of knowledge and opinion about animal behavior. The author exhibits real insight into animal psychology, a quality missing in the writings of some workers in the field of animal behavior, whose striving for complete objectivity results in nothing more important than complete heuristic sterility. We agree with Professor Claparède, who says in introducing the book that it ought to be read by all psychologists, veterinarians, breeders, hunters, trainers, horsemen, and lovers of animals generally, on the ground that it will teach them how better to appreciate animals.

THE PSYCHOLOGY OF INDIVIDUAL DIFFERENCES.

By Robert S. Ellis. D. Appleton and Co.
\$3.50 $5\frac{1}{4}$ x 8; xxiv + 533 *New York*

Covers the whole range of matters concerned with the question of psychological differences, in the typical manner of text book condensation. As merely ancillary to the treatment of the main topic, are taken up in successive chapters such subjects as the relation between body and mind, the analysis of the individual, statistical methodology, mental measurements, heredity. All the ideas are categorically labelled in the 523 pages contained in the book, about 1.8 ideas per page on the average. There is an index.

MOTIVE FORCES OF THE MIND.

By Alice Raven. W. Heffer and Sons, Ltd.
3 s. 6 d. net 5 x $7\frac{1}{2}$; vii + 94 *London*

This is a brief, well written account of the dynamic aspects of modern psychology, written primarily for an audience of women, chiefly settlement workers in East London. The point of view, and the sources drawn upon, are mainly British. The discussion is sound and well balanced.

The book will be useful to the busy worker in other fields of science, who wishes, in an hour or two of reading, to gain some idea of what psychology has to say today regarding the practical working of the minds of themselves and of other people. There is no index.

HOW ANIMALS FIND THEIR WAY ABOUT. *A Study of Distant Orientation and Place-Recognition.*

By Étienne Rabaud. Translated by I. H. Myers. *Harcourt, Brace and Co.*
$2.75 $5\frac{3}{8}$ x $8\frac{1}{2}$; 142 *New York*

A review of the literature regarding orientation in animals which comes to the conclusion that nothing more than the ordinary sense and motor organs of the body are required to account reasonably for the known facts. Chapters are devoted to orientation in flying and walking insects respectively; in other invertebrates; and in vertebrates. The book contains a bibliography of 71 titles, and an index, but not much new.

THE PROBLEM OF LAY-ANALYSES.

By Sigmund Freud. *Brentano's*
$2.50 5 x $7\frac{1}{2}$; 316 *New York*

A consideration of at least some slight weight that would appear to bear against Freud's doctrine of the all-importance of the sexual interest for individual psychology is provided in his autobiographical sketch given in the latter half of this book. At only one point in the author's career when he *hurriedly* finished off a beginning work on cocaine in order to visit his fiancée, the sexual impulse seems to have been in the ascendant; otherwise his life appears to have been a steady drive of the scientific intellect. Always brilliant, he early made a reputation as a diagnostician and had achieved notable work in the field of neuropathology before his interest became focussed on psychiatry. After an initial period with Charcot and Janet, he tells of the gradual evolution of the body of ideas that are now well known under the name of psychoanalysis, and reveals a mind of great originality and tremendous courage. As to the enduring validity of his theories there may be much doubt, but at the very least he has taken psychopathology out of its academic ruts and given it dynamic quality.

The first part of the book is devoted to an advocacy of the participation by properly prepared laymen and women in the practice of psychoanalysis. The argument is presented in Socratic manner, as a conversation with a hypothetical Referee. It is not convincing.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

SCEPTICAL ESSAYS.

By Bertrand Russell.
W. W. Norton and Co., Inc.
$2.50 $5\frac{5}{8}$ x $8\frac{3}{8}$; 256 *New York*

This is an enormously entertaining book about a variety of subjects. Few if any living persons are so nimble of wit as its distinguished author. Nobody has to agree with him to enjoy the book. But if censors had sense they would suppress it at once, because a book more subversive of all that upright, good, forward looking Methodists and Baptists and Presbyterians are pleased to look upon as sound spiritual values was never printed. How stupid censors are! They will throw to the wolves a book that hasn't an idea in it, good or bad, if it contains once a word of four letters that every child knows and is wholly undisturbed by. On the other hand a book like this one, which contains no such word, may circulate freely, regardless of the fact that it will permanently and incurably poison the mind of any young man or woman who reads it.

Take for example the essay on "Good Men."

> We all know what we mean by a "good" man. The ideally good man does not drink or smoke, avoids bad language, converses in the presence of men exactly as he would if there were ladies present, attends church regularly, and holds the correct opinions on all subjects. He has a wholesome horror of wrongdoing, and realizes that it is our painful duty to castigate Sin. He has a still greater horror of wrong thinking, and considers it the business of the authorities to safeguard the young against those who question the wisdom of the views generally accepted by middle-aged successful citizens. Apart from his professional duties, at which he is assiduous, he spends much time in good works: he may encourage patriotism and military training; he may promote industry, sobriety, and virtue among wage-earners and their children by seeing to it that failures in these respects receive due punishment; he may be a trustee of a university and prevent an ill-judged respect for learning from allowing the employment of professors with subversive ideas. Above all, of course, his "morals," in the narrow sense, must be irreproachable.

Having so accurately defined a "good" man Russell presently proceeds to discuss his usefulness. For example:

> Another of the uses of good men is that any undesirables can be kept out of politics by means of scandals. Ninety men out of a hundred commit breaches of the moral law, but in general this fact does not become public. And when in the ninety-ninth case it becomes known in relation to any individual, the one man in the hundred who is genuinely innocent expresses genuine horror, while the other ninety-eight are compelled to follow suit for fear of being suspected. When, therefore, any man of obnoxious opinions ventures into politics, it is only necessary for those who have the preservation of our ancient institutions at heart to keep track of his private activities until they discover something which, if exposed, will ruin his political career. They then have three courses open to them: to make the facts known and cause him to disappear in a cloud of obloquy; or to compel him to retire into private life by threats of exposure; or to derive for themselves a comfortable income by means of blackmail. Of these three courses the first two protect the public, while the third protects those who protect the public. All three, therefore, are to be commended, and all three are only rendered possible through the existence of good men.

HISTORY OF THE SHEFFIELD SCIENTIFIC SCHOOL OF YALE UNIVERSITY. 1846–1922. *Vols. I and II.*

By Russell H. Chittenden.

Yale University Press
$10 for two volumes *New Haven*
6½ x 9¾; xix + 610

In preparing the material for these two beautifully printed and illustrated volumes Professor Chittenden has performed a notable service for the history of science in America. Yale University and its Sheffield Scientific School have played an important rôle in the development of science, and particularly of technical education in this country.

The Sheffield Scientific School has a separate board of trustees, and separate endowment funds. Certain difficulties between the University and the School have arisen, apparently as a result of entirely natural processes, which Professor Chittenden fully describes. It does seem a pity, however, that such a fine record of important achievement should end on the following note: "What the future of the Sheffield Scientific School is to be depends largely upon the attitude of the Corporation of the University. Under the conditions now imposed the future looks dark. But what will be the verdict of thoughtful people upon a line of action which results in the dissolution of a once progressive and powerful institution, a part of Yale University, of which there was much to be proud? Will memory of the accomplishments of the past be the only remainder of a school of science that played so important a part in the development of scientific education and scientific research in this country, from the middle of the nineteenth century on?"

A SHORT HISTORY OF MEDICINE.

Introducing Medical Principles to Students and Non-Medical Readers.

By Charles Singer. Oxford University Press
$3.00 $5\frac{3}{8}$ x 8; xxiv + 368 *New York*

For wide scope of interest, deep learning and original research, the author of this little book stands foremost among historians of science writing in English. His continued devotion to writing for the general public is to be gratefully welcomed. The great cultural value of the history of science is still insufficiently appreciated. Skepticism of finality in thought and toleration of differences of opinion stand out as the moving forces in the history of scientific progress, and these qualities were never more needed in our policy than now.

Far from being a dry compendium of historical names and dates, the book emphasizes what the author calls the philosophy of medicine, by which he means its underlying principles rather than details of practical application. He traces the development of medical thought from the Greek period through modern times. Notable is the large proportion of space he devotes to recent history, more than half of the book being given over to modern medicine. The book is generously illustrated and has a good index.

THE GRAPHIC BIBLE *from Genesis to Revelation in Animated Maps and Charts.*

By Lewis Browne. The Macmillan Co.
$2.50 8 x $10\frac{3}{8}$; 160 *New York*

The talented author of *This Believing World*, noted in these columns earlier, has again put us in his debt by condensing the essence of the Bible as a narrative into a space of 160 pages, with an illustration from his own gifted hand on nearly every page. These illustrations are chiefly maps, which somehow convey a sense of reality as to place and time which we venture to think is sadly lacking in most biologists' knowledge of the events discussed in the Bible. Therefore we strongly commend this book to their attention. Aside from its great practical usefulness it is entertaining.

A POCKET MEDICAL DICTIONARY.

Giving the Pronunciation and Definition of the Principal Words Used in Medicine and the Collateral Sciences Including Very Complete Tables of the Arteries, Muscles, Nerves, Bacteria, Bacilli, Micrococci, Spirilla, and Thermometric Scales, and a Revised Dose-list of Drugs and Their Incompatibilities, in the English and Metric Systems of Weights and Measures, Based upon the Tenth Revision U. S. Pharmacopoeia; also a Revised Veterinary Dose Table.

By George M. Gould.
P. Blakiston's Son and Co.
$2.00 $3\frac{1}{2}$ x $6\frac{1}{8}$ *Philadelphia*

A new edition of this standard dictionary, incorporating a selection of recent accessions to medical terminology. This pocket edition contains 40,000 words, is durably bound and handy as a ready reference where a comprehensive and detailed definition is not essential.

EDITORIAL NOTE

The time seems to have come when it is desirable to make a formal and authoritative statement regarding the *New Biological Books* Section of The Quarterly Review of Biology. This section appears to have met with rather widespread approval from the biological reading public since its inception, so far as the Editors have been able to judge from correspondence and conversation with scientific colleagues, and from the frequently so earmarked growth of the subscription list. This leads the Editors to suppose that the general editorial policy of this section has, on the whole, been favorably regarded by biologists generally. An occasional sour note has been heard from an author who thinks he has been unfairly treated in the notice of his book, but every such letter in our files is matched by at least one letter (and often more) from an equally distinguished biologist expressing hearty approval of the particular review in question.

One important element in the editorial policy relative to the book reviewing section of The Quarterly Review of Biology has been that all reviews shall be anonymous. This anonymity has been preserved, and will be, with the utmost fidelity.

It has increasingly been made apparent to us, however, that there prevails a widespread notion that the Editor writes all, or substantially all, of the book notices appearing in this Review. The chief purpose of this note is to correct this misapprehension. The Editor of The Quarterly Review of Biology writes only a small fraction of the book notices which appear in its pages. The book reviews not infrequently express judgments and opinions entirely contrary to those of the Editor regarding the books concerned.

The Editors wish further to take this opportunity to state categorically that they assume no responsibility for opinions expressed or conclusions reached by authors of signed articles printed in The Quarterly Review of Biology. Articles are accepted for publication because the Editors regard them as likely to be of interest, or of use, or both, to the biological public, and for no other reason. This is the total extent of the editorial responsibility. Outside of these limitations any writer in The Quarterly Review of Biology is at liberty to say anything he likes. The responsibility for his utterances is his, not ours. We sometimes try to help him put his views in a form consonant with the literary and artistic standards which we try to maintain in the Review, but *scientifically* he digs his own grave and erects his own monument.

R. P.

VOL. IV, NO. 3 SEPTEMBER, 1929

THE QUARTERLY REVIEW *of* BIOLOGY

THE CYTOLOGY OF GLANDULAR SECRETION

BY ROBERT H. BOWEN

Department of Zoölogy, Columbia University

(*Editorial Note:* While this paper was passing through the press Dr. Robert Hall Bowen died, at the age of thirty-seven, after a very brief illness. The loss to biology from the passing of this brilliant young investigator, just at the start of a career of extraordinary promise, is irreparable.)

INTRODUCTION

> Pour nous, histologistes ou histophysiologistes, la sécrétion consiste essentiellement dans l'élaboration au sein du protoplasma des cellules d'un matériel spécial qui caractérisera le produit de sécrétion de la glande.
>
> (Ranvier, 1887.)

IT IS a striking characteristic of metazoan cells that at some stage in their history structures of various kinds are built up in the cytoplasm. This phenomenon—differentiation— results in making cells histologically diverse. Thus in certain cells muscle-fibrils appear, in others neurofibrils and Nissl substance, yolk, and so on. Of these differentiation-products some are relatively permanent, as in muscle or nerve cells, and become an integral part of the cell containing them. In other cases, however, the products of differentiation are transitory and may disappear again into the cytoplasm from which they seemed to be evoked—as in case of yolk in a developing egg; but more commonly such products are formed only to be eliminated from the cell like the zymogen granules of the pancreas. Broadly speaking, therefore, the problem of "secretion" is not confined to the evacuation of a fluid, as usually conceived by the physiologist, but includes all that large group of phenomena in which materials of many kinds are elaborated in the cytoplasm only to be returned to the cell-system, or else extruded as a part of some secretion. The problem of glandular secretion thus shapes itself for the cytologist in terms decidedly different from those to which the physiologist is accustomed. "Secretion," for the cytologist, has nothing to do with mere extrusion from the cell, but refers rather to those recondite processes by which the cell elaborates the specific elements of the extruded material. This contradiction in terms was pointed out by Ranvier as long ago as 1887, and is doubtless traceable to the fact that the flow of liquid from a gland was studied long before even the cellular basis of living matter was suspected. Quoting Ranvier ('87, p. 13):

> Par exemple, si l'on excite par un courant d'induction interrompu le nerf sécrétoire d'une glande muqueuse, on voit l'excitation du neuf suivie d'une abondante sécrétion. C'est l'acte sécrétoire des physiologistes. Pour eux, la sécrétion d'une glande muqueuse ne consiste pas dans l'élaboration du mucigène au sein des cellules, mais dans la formation et l'issue du mucus. Or, si l'on analyse le phénomène, si, au lieu de prendre le résultat entier du travail glandulaire, on considère le phénomène histologique, on est porté à penser, au contraire, que la sécrétion consiste dans l'élaboration du mucigène et que ce que les physiologistes appellent sécrétion n'est qu'un phénomène d'excrétion.

Unfortunately, the term "excretion" has come to have a rather definite meaning, quite different from that suggested by Ranvier, and J. Müller's distinction between an "excretion" and a "secretion" is still largely followed. Thus the essence of a secretory process, namely, the origin of the substances specific to glandular products, has been neglected by the physiologist, and he has felt no need even to name a process of which he takes practically no cognizance. But it is exactly this aspect of the problem which interests the cytologist, for whom even the "excretions" of physiological terminology may in many cases belong to his broader category of "secretions."

Whether there is any real significance in these distinctions may perhaps best be left undecided, but for practical purposes we must come to some terms with these differences in current usage. In this review I shall accordingly follow Ranvier, and restrict the term "secretion" to the process of intracellular synthesis. Similarly the process of extrusion, or the emptying of a gland-cell, will be called "excretion." It may be noted that these difficulties in terminology led Matthews ('99) to suggest that "secretion" be retained in its present physiological sense, and that the synthetic process within the cell be termed "hylogenesis." I am inclined to believe that some such solution of the difficulty may eventually prove most feasible.

The present review proposes to deal only with the secretory phenomena in so-called glandular cells. Even in so limited a category of cells, it is a moot point as to whether secretion is invariably an expression of one essential process, or whether in different types of glands, different morphological origins are to be expected. It is my own feeling that the phenomena of glandular secretion are based on some plan common in its essentials to all gland-cells. The more we learn about the cell, the more evident does it become that a given life-process, at first described with many patterns, is gradually resolved into numberless variations of a single basic procedure. With expanding horizons, the unity of a particular cell-activity seems ever more significant. It is, therefore, safe to suggest that experience should caution us against the easy acceptance of accounts of cell-mechanisms for secretion, which are diametrically opposed. The fact that two cells produce radically different secretions scarcely warrants the assumption that the mode of production can also be fundamentally different in the two cases. Cytological interpretations of particular secretory cells, which take no account of the known elements of both cytoplasm and nucleus, and neglect to seek for some wider correlation with the varied aspects of secretory phenomena in general, forfeit, it seems to me, any claim to serious consideration at the present time.

The cytological problems presented by secretory activity have for many years offered an attractive field for investigation, but they have in recent years assumed an added interest in the light of suggestions that the mechanism for the elaboration, for example, of digestive enzymes, may likewise be the source of hormones and those little known intracellular enzymes upon which metabolism seems to depend (Bowen, '24a; Wilson, '25). It is, indeed, conceivable that an exact knowledge of the more obvious phenomena in gland-cells might carry us far toward an understanding of those less conspicuous but more important secretory phenomena which are the common property of all cells.

HISTORICAL ORIGINS OF THE PROBLEM

> Das Blut enthielt in sich schon alle Bestandtheile aller Secrete präformirt.
>
> (Statement of 18th century point of view by R. Heidenhain, 1883.)

> Es sind . . . . nicht die Blutgefässe, welche secerniren, sondern die Wände der überall geschlossenen Drüsenräume, auf welchen die Blutgefässe ein Netz bilden. Die Drüsen stellen in ihrem Innern eine im kleinsten Raume construirte grosse Oberfläche dar; die diese bekleidende lebendige Substanz ist es, welche die Sekretion einleitet.
>
> (Paraphrase by R. Heidenhain (1883) of the view of J. Müller, 1830.)

> Car, pour nous tous, il est absolument évident que la sécrétion n'est pas un acte de simple filtration, comme on le croyait naguère, mais un phénomène essentiellement cellulaire, et que, si l'on savait ce qui se passe dans les cellules essentielles d'une glande, on connaîtrait parfaitement la fonction physiologique de cette glande.
>
> (Ranvier, 1887.)

The production of fluid or semifluid material in connection with definite organs (glands) has of course long been known, and during the 18th century with the advance in general knowledge of the human body and its functions, a serious attempt to put glandular phenomena in harmony with other anatomical knowledge first emerges. According to Ruysch and others, there existed direct connections between the excretory ducts of a gland and the vascular system, the blood itself being presumed to contain preformed all kinds of secretory products. Depending now on the nature of the vascular arrangements, their length, width, etc., in this gland or that, specific constituents of the blood stream were separated out, squeezed by the pressure in the blood vessels through sieves of different apertures. For an extended exposition of these 18th century viewpoints, reference may be made to Haller, Elementa physiologiae II. liber VII, Lausannae, 1760.

Although opposed to the conclusions of Malpighi and many others, such views persisted into the 19th century, until J. Müller in 1830 arrived at a better understanding of the secretory process. Müller rejected the vascular theory and held that the active agent was the living substance which lined the walls of the glandular lumina, the blood-vessels merely forming a superficial network. Differences in the secretory product were traced to those differences in living substance familiar in organs of various kinds. The gross structure of a gland was dismissed as having no bearing on the essential problem.

At this point the cell-theory appeared, followed by immediate efforts to reduce glandular structure to a cellular basis (Henle, Müller, etc.), a result first clearly established by Dujardin (beginning in 1837), although Dutrochet already in 1824 had written, "la cellule est l'organe sécréteur par excellence." For an interesting historical review refer to Milne-Edwards ('72). From the work of the two following decades, it became gradually clear that glands are composed of cells in varied arrangements, although in Kölliker's *Mikroskopische Anatomie* of 1850, their relation to the secretory process was not yet resolved.

Coincident with these early attempts to correlate the cell-theory with glandular flow, was another development which had its origin in the work of Dutrochet and

Jolly on membrane-diffusion. The obvious possibilities of arriving at once at a physical explanation of glandular activity were eagerly grasped, and eventuated in the physical view developed by Ludwig in his *Lehrbuch der Physiologie* (1856).

It was peculiarly the contribution of R. Heidenhain ('66 to '83) to bring back into clear focus the essential part in glandular activity played by living substance—the individual cell—and to express this in terms at once useful to both cytologist and physiologist, avoiding a too facile mechanical explanation on one hand, and, on the other, an explanation which loses itself in obscure "vital forces."

THE INDIVIDUAL CELL AS THE BASIS OF GLANDULAR ACTIVITY

> . . . dass die Sekrete kein Caput mortuum, sondern die Producte der chemischen Thätigkeit lebender Zellen sind.
>
> (Nussbaum, 1877.)

> En réalité, toutes les glandes, mérocrines et olocrines, présentent un mécanisme analogue de la sécrétion . . . . Ces termes de mérocrines et olocrines se rattachent à un processus qui caractérise plûtot une des phases ou un des modes de l'excrétion que la sécrétion proprement dite.
>
> (Ranvier, 1887.)

That differences in the "contents" of gland-cells correspond in some way to differences in the excretion-products of glands was suggested by Henle in 1841, but the first clear proof that gland-cells actually contain part of the excreted material, visibly preformed, in the cytoplasm, was given by Goodsir in 1844, in case of the ink of cuttlefish, a case of special interest since secretions with a distinct color are not common in animal cells. (For a few examples see Solger ('94).) The further fact that in sebaceous glands the cells become laden with fatty secretory products and that the ensemble is lost at the time of excretion was completely described by Kölliker in 1850. Many other workers (e.g., Leydig, '57; Schulze, '67) saw secretory products within the gland-cell and clearly recognized that they were subsequently extruded as an essential part of the familiar glandular products. Nevertheless, the general relation between preformed intra-cellular secretions and the visible products of an active gland was for many years a subject of controversy. For a proper appreciation of the difficulties which were encountered in early attempts to understand the exact connection between the product of a particular gland and the living material which constitutes its cellular substratum, it is necessary at this point to consider certain features of the excretion-process.

It is clear now, after long controversy, that gland-cells may evacuate their secreted contents in several different ways. As suggested by Ranvier's classification, there are two extreme types of behavior—holocrine and merocrine.

The simplest type is the holocrine gland, which has as a product the cells themselves with all their enclosed secretion. Such are the sebaceous glands of mammals, and avian oil-glands. In merocrine glands, on the other hand, the secretory products are released, washed out as it were, from the individual cells, which themselves are left to repeat the process. There are many intermediate conditions in which lobes of the cell-periphery, laden with secretion, are broken off in toto, as in mammary glands, certain Harderian glands, etc. This mode of excretion is often called "blasenförmige Sekretion" (cf. Henschen ('04), Mislawsky ('09), Brinkmann ('12), Schiefferdecker ('17), but it appears that this name has also been applied rather loosely to many cases in which the excretory processes are somewhat different, as for example the case described by Van Gehuchten ('90), often termed "tropfenförmige Sekretion." It is now clear that in the final analysis all these differences have little significance, for soon or late individual cells of the merocrine type "wear out" and doubtless also go to pieces to be lost in the general glandular product, their places being taken by new cells.

Unfortunately, to earlier workers the true import of the excretion-phase in holocrine and merocrine glands was entirely missed and the essential unity of secretory phenomena was obscured by the belief that the holocrine gland-cell is undergoing a degenerative process which reaches its culmination in the loss of the whole cell. This view was first sponsored by Virchow ('57), who compared the fatty material in a sebaceous gland to the products of "fatty degeneration" familiar to pathologists. Brinkmann ('12) and others before him have even been led by this interpretation to consider the exclusion of sebaceous glands from the category of "true" glands, holding (Brinkmann) that the fatty material results from necrobiotic changes due to unfavorable relation to sources of oxygen and food. This whole phenomenon, according to Brinkmann, is to be contrasted with the "vital" processes in other gland-cells—whatever that may mean. In any event, the nature of the cell-cycle having been so early and so clearly made out in these typical holocrine cells, it was natural that somewhat similar views should arise in explanation of the phenomena in other glandular types (e.g., in goblet-cells, Schulze, '67). And, as a matter of fact, it has since become evident that the holocrine type of behavior is by no means limited to glands of lipoidal secretion.

From such a background emerged the view originally held by R. Heidenhain ('68), that the gland-cells become filled with secreted material, which is discharged together with the cell when the gland becomes active, cell and secretion being washed out by the fluid which, released from the capillary stream, forms the substratum of the glandular discharge. In other words all gland-cells would in the final analysis belong to the holocrine type. Or as Ogata ('83) put it, the gland can only function as it destroys certain cells and builds new ones in their stead. These views are in essence only an extension of Cl. Bernard's old theory of living processes, according to which the cell builds incoming materials into living protoplasm—a part of itself—and differentiations then emerge only by transformation of the living substance proper. Pflüger ('66), on the other hand, held that the gland-cell produced secretions from which it freed itself at stated moments, returning then to its primitive condition to repeat the cycle of storage and discharge. The living protoplasm itself was not directly transformed into secretion-product (cf. Galeotti ('95), Krause ('95), Kolossow ('98), etc.).

The ensuing controversy expressed itself in a voluminous literature, summaries of which can be found in Van Gehuchten ('90), Galeotti ('95), and Oppel ('00), and even today the excretion-process in those gland-cells which are not obviously of the holocrine type, is in many cases incompletely known. However, the key to the matter was found by a pupil of Heidenhain, Lavdovsky ('77), who concluded that glandular activity (in merocrine gland-cells) involved features of both views. Thus he held that gland-cells were maintained in normal activity (in Pflüger's sense) for a longer or shorter period, but were in the end of a "transitory" nature and must finally be lost with the excretory product. The actual discharge from a gland-cell of the secreted material and the correlation of the fluctuations in amount of secretion contained in the cell with different phases of secretory activity, were finally demonstrated by Langley (and Sewall) in a long series of papers dating from 1879. In its essentials this represents our present conception of cellular history in merocrine glands, the actual length of life of a given cell and the exact method of replacement being still very imperfectly understood.

Thus have modern views of the gland-cell gradually taken shape. It is now clear that the gland-cell is in reality a "secretory" cell, which lends to the glandular products their characteristic essence through the intermediary of chemical transformations effected in some way within the cell itself. The general course of events is presumably based upon a common pattern, and to this extent all gland-cells are but variations of a single cell-type. The superficial differences which gave rise to the terms holocrine and merocrine, refer not to the secretory, but to the excretory, activities of the cell. And to this extent these terms apply to a physiological rather than a cytological problem. In all cases there is deposited in the cytoplasm of the gland-cell, as a product of cellular activity, a characteristic secretion-material. This is then discharged by the loss of the whole cell (holocrine type), or is "washed" out of the cell together with an abundance of fluid abstracted from the vascular stream, the living cell-substance proper remaining behind essentially intact (merocrine type).

I ought perhaps to digress at this point from the main course of the discussion to point out that in many holocrine glands (sebaceous type) the "degeneration-theory" is still too widely accepted as an explanation of their activity. It therefore seems worth while to emphasize the fact that the data now available provide a conclusive demonstration of the inadequacy of any such view. Secretion in a sebaceous gland-cell is a synthetic process essentially akin to that in mucous or serous cells. This was first clearly indicated by the classical studies of Altmann ('94), whose main conclusion has been corroborated by many later workers (Michaelis ('98), Ottolenghi ('01), Bab ('04), Stern ('05), Kuć-Staniszewska ('14), Ludford ('25b), Bowen ('26b)). It is high time to abandon the outworn catchwords of "fatty degeneration" as an explanation of the secretory phenomena in sebaceous glands.

THE MORPHOLOGY OF SECRETION

> Eine merkwürdige Erscheinung bei der Umwandlung des Zelleninhaltes ist, dass häufig die Bildung gewisser Sekrete in eigenen, innerhalb der Zelle liegenden Bläschen, den "Sekretbläschen" erfolgt.
>
> (Leydig, 1857.)

> Alle Beobachtungen . . . . bestätigen daher den einen Satz: Die Secretion ist ein granulärer Process . . . .
>
> (Altmann, 1894.)

When gland-cells are studied in the fresh condition, or after fixation and staining, their microscopic appearance varies with the kind of cell and the method of preparation. To most earlier workers the morphological details of a gland-cell seem to have been of little interest, and they speak rather casually of the "contents" of the cell as clear, transparent, granular, a network containing vacuoles, etc.; and they refer the origin of such appearances to "schleimige Metamorphose," "dégénérescence muqueuse," "fatty degeneration," and the like. It was clearly recognized that chemical changes within the secretory cell found expression in various morphological appearances of the cytoplasmic area. These appearances were particularly commented upon during the period between Heidenhain's initial work (1866–68) and the development of Altmann's granular theory, which reached its final expression in 1894. The results of this period are exhaustively reviewed by Oppel ('00) for the glands of the buccal cavity and the pancreas; by Paneth ('88) in case of goblet cells, and by Nicolas ('92) and Galeotti ('95). The occurrence of definite granules in the pancreas-cell had been noted by many observers since 1850 (at first under the name of fat granules), and a granule-structure was also observed particularly by Langley ('79–'89) in serous and mucous cells (salivary). Langley, Heidenhain, and Nussbaum ('77–'86) observed cells in both the living and fixed condition, and came to the conclusion that the granules represented secretion-products which were evacuated during the excretory activity of the cell, and were in some sense the source (after dissolution) of the characteristic qualities of the fluid from a particular gland. The first complete account of this phenomenon was the work of R. Heidenhain ('75) on the pancreas. In 1879 Langley wrote, "That is, during secretion the granules normally contained by the cells, are in some way or other used up, probably to form part of the saliva [in this case] secreted." See also Kühne and Lea ('82). It is, however, to be noted that it is not necessary to suppose that in the pancreas, for instance, the zymogen granules are themselves the forerunner of the pancreatic enzymes, but are merely the physical substratum in which the inactive enzymes are somehow contained (e.g., Lewaschew, '85). Similar views were espoused by many other workers during the period from 1880 to 1890—for example, the "Sekretbläschen" of Leydig ('57), the "Drüsenkörner" of Schwalbe ('72), the "Sekrettropfen" of Platner ('89), Paneth ('88), and the "Primärgranula" of M. Heidenhain ('90). An extended list of similar references will be found in Galeotti ('95), Nicolas ('92); also Müller ('96). Nevertheless the whole matter remained in a somewhat chaotic state due primarily to the fact that while in some glands, like the pancreas, the granular condition of the secretion is readily demonstrated, in other glands (mucous cells in particular) the granular appearance is usually obscured.

The real nature of the secretion-process was first clearly elucidated by Altmann, whose extended observations established the occurrence in the cytoplasm of discrete granules (or vacuoles) as the universal characteristic of secretory cells. Altmann ('94) concluded that secretion is always a granular process and subsequent observation has led increasingly to the establishment of this opinion as the correct explanation of gland-cell morphology. An excellent historical sketch of the emergence of this, the so-called "Granulalehre" as applied to gland-cells, is given by M. Heidenhain ('07), pp. 333 et seq. The facts were, indeed, already in process of clear generalization in 1899 (Harrington). Papers of this period in which the granule doctrine emerges with varying degrees of understanding are those, for example, of Nicolas ('92), Saint-Remy ('92), Nicoglu ('93), Galeotti ('95), Müller ('96), Solger ('96), Weiss ('99), Ellermann ('00), Noll ('01), Schmincke ('03), and Fleischer ('04).

The cytologist, therefore, finds it always possible to observe (at some stage) in a gland-cell a congeries of "granules" which constitute the "secretion" produced by the cell. There are a few anomalous exceptions to this rule (e.g., Carlier ('05), Eklöf ('14), Benoit ('20), Saguchi ('20a)) in which unformed secretions have been described, but the status of these observations seems to me decidedly doubtful. When the gland excretes, the whole cell may be lost as in the holocrine type, or the granular area only may be swept out by a current of watery fluid passed through the cell from the blood or lymph capillaries adjacent to its base. In some cases the granules are excreted intact, but in the majority of cases they are dissolved in the outgoing stream at the moment of excretion, or may undergo more or less fusion and "solution". (?) within the cell prior to the beginning of excretion. For an understanding of the secretory process, however, these variations are of secondary interest.

Specific attention should perhaps here be drawn to the fact that the "granules" are not necessarily the only cellular contributions to the excretion-product of a gland. Clearly, in holocrine glands, the product includes at least remnants of all the cell-structures. It is likewise probable that during excretion there is in all gland-cells some loss of the cellular substrate. Just what such cellular contributions will be in a particular instance, is probably to a certain extent a matter of chance. In any event, it has not been shown that they have any significant part to play in the glandular product as a whole; and the inclusion of fragments of the Golgi apparatus, chondriosomes, extruded nuclei, etc., seems quite lacking in the importance which some observers have attached to this phenomenon.

The exact method by which excretion itself is accomplished undoubtedly differs in different glands, as is sufficiently indicated by the mere occurrence of the holocrine and merocrine conditions. The problems thus raised fall, however, rather within the field of the physiologist than of the cytologist. For discussion of the views which have been proposed, refer, for example, to Ranvier ('86–'88), Van Gehuchten ('90, '91), Gilson ('90), Kolossow ('98), Mathews ('98), Zimmermann ('98), Henry ('00), Brinkmann ('12), Heidenhain and Werner ('24), and Benoit ('26). Here also may be noted the occurrence of so-called secretory capillaries which sometimes penetrate into the cytosome and presumably serve as extensions of the duct-system by which the glandular products are evacuated. For discussion of older literature on this subject see R. Heidenhain, ('83), and Kölliker ('89), and for the later work, Cajal ('89), Fusari and Pansci ('90), Golgi ('93), Müller ('92, '95, '98), Solger ('96), Stöhr ('96), Krause ('97), Kolossow ('98), Oppel ('00), Browicz ('02), Fleischer ('04), and Arnold ('08).

The morphology of the "granules" which are thus the essential product of secretion, has been little studied, and only very recently have the possibilities of a generalized analysis received adequate attention. These possibilities find their source in old accounts like those of Meckel ('46) and Leydig ('57), who observed the formation in certain secretory cells of definite, intracellular vesicles or vacuoles (Sekretbläschen). Altmann ('94) subsequently recognized that his secretory grannules were often divisible into a central substance and a peripheral layer (or vacuole). A similar state of affairs seems to have been partially grasped by Nicolas ('92), who described the secretion-bodies as vacuoles (of liquid content) each enclosing a granule (see also Flemming ('82), Stöhr ('87), Held ('99), Fleischer ('04)). These scattering observations were finally brought to a focus by Renaut ('07), who undertook an analysis of the structural details of secretions, which he subsequently ('11) embodied in a very readable account of secretory processes. He pointed out in the first place that the simplest type of secretory activity was expressed by the formation and growth of a vacuole or droplet of permanently homogeneous material, fluid or semi-fluid in nature. This, Renaut termed the plasmocrine mode of secretion. A more complicated method involves the formation of a minute granule around which a vacuole forms, and as the vacuole enlarges it serves as a minute reservoir in which specific products of cellular activity are accumulated and gradually concentrated by addition to the central granule. This granule he called a "grain de ségrégation," and the whole process constitutes the rhagiocrine mode of secretion (fig. 1). Still other modes of secretion were defined in his paper, but these seem of decidedly less general interest.

It is now becoming increasingly evident that secretion is essentially a vacuolar phenomenon, the great majority of cases resulting in the production at some stage of a central granule (rhagiocrine mode). Clearly the "granules" of older workers were sometimes secretory vacuoles in which the granules proper were not demonstrated, in other cases the granule alone was demonstrated, and in some cases the ensemble was correctly made out. In serous cells, the granule-within-a-vacuole structure is often easily demonstrated, while in mucous cells special staining is usually required. Furthermore, the growth of the granule may continue until it fills the entire vacuole, which is itself obliterated (fig. 1 *G*). This occurs very quickly in the vertebrate pancreas, while in the serous cells of many kinds of salivary glands the enclosing vacuole may be retained for a long period, perhaps permanently (e.g., Bowen, '26a). Not infrequently the granules go through a process of ripening or maturing, often involving special features of morphology and staining capacity (e.g., Altmann, '94; Heidenhain, '07; Bowen, '26a, etc.).

This duplex structure of each secretory droplet has been recently interpreted in general terms by Parat ('28), Bowen ('26d), and others, in the following manner (fig. 1). The vacuole first arises as a watery droplet separated from the rest of the cell-substance by a limiting surface-membrane of some kind. Across this membrane pass secretory materials which have been elaborated by cellular activity and, becoming concentrated within the vacuole, are finally deposited in the form of the familiar "segregation granule." In this simple procedure the morphological essentials of secretory phenomena seem at last to have found an adequate basis.

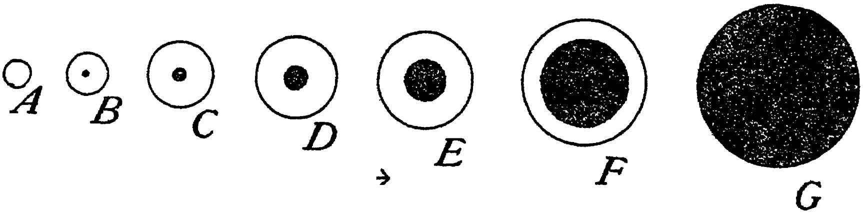

FIG. 1. PROGRESSIVE SERIES OF STEPS IN THE PRODUCTION OF A SECRETORY DROPLET OF THE RHAGIOCRINE TYPE

The secretory granule proper is stippled; its size with respect to the enclosing vacuole has been drawn somewhat too small in order clearly to bring out the topographical relations. In many cases the granule may be eccentrically placed within the vacuole, a condition not shown in this diagram.

Finally, with respect to the physiological interpretation of the origin of secretions, two views have been held, based to some extent on an author's opinion as to whether glandular excretion involves the total breakdown of the cell or not. According to one view, derived from Claude Bernard's theory of vital activity, the secretory droplets arise by direct chemical transformation of protoplasm. According to the other view, well expressed by Pflüger ('66), the gland-cell builds secretory products through the intermediary of a special synthetic activity, being then capable of freeing itself at definite times of these products, whereupon the cell returns to its original condition and repeats the process. Or as Haeckel expressed it, the cell behaves like a plast. Not only does this second view of secretion seem necessitated by modern trends in the theory of cellular physiology, but, as will later appear, it is the only view in harmony with the morphological findings.

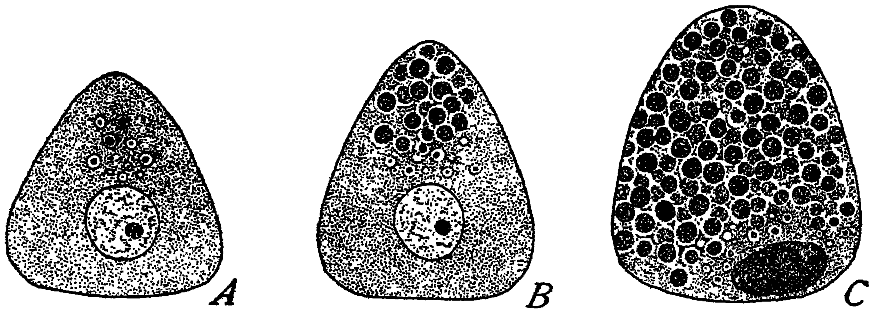

Fig. 2. Successive Steps in the Secretory Cycle of a Gland-cell (Diagrammatic)
A, first appearance of secretory products at the beginning of a cycle of synthetic activity; *B*, intermediate stage in the formation of secretory droplets; *C*, final stage, shortly before excretion begins.

THE SECRETORY CYCLE

> In denjenigen Drüsen, bei welchen Perioden der Thätigkeit mit Zeiträumen der Ruhe abwechseln, lassen die secernirenden Zellen Unterschiede ihres innern Baues erkennen, welche für den ruhenden und den thätigen Zustand charakteristisch sind. . . . Zu bestimmten Zeiten nimmt die Zelle aus dem allgemeinen Ernährungsmateriale des Blutes oder vielmehr der Lymphe bestimmte Substanzen auf, zu bestimmten Zeiten setzt sie dieselben in bestimmter Weise um, zu bestimmten Zeiten giebt sie die Umsetzungsproducte nach Aussen hin ab.
>
> (R. Heidenhain, 1883.)

That gland-cells must pass through internal changes, which in their totality comprise a "secretory cycle," eventuating in the discharge of a secretion, was early recognized in case of sebaceous glands and others which were supposed to be of a similar type (goblet cells, for example, Schulze, '67). But that all secretory cells exhibit changes in appearance correlated with excretory stimuli was for a long time unrecognized. It seems to have been hinted first by Claude Bernard in 1864, but it is generally agreed that the initial contributions to this problem were the classical papers of R. Heidenhain extending from 1866 over a period of fifteen years. Heidenhain, adopting a histophysiological approach to the problem, demonstrated that when a gland was stimulated its cells underwent a change in appearance, thus definitely proving for the first time in many kinds of glands that secretory activity is directly linked with activities of the cells themselves. The real nature of the change was further elucidated by Lavdovsky ('77) and particularly by Langley ('79, etc.), not to mention the work of many others, an extensive bibliography of which is given by Oppel ('00).

It is now clear that in the beginning the cytoplasm of a gland-cell is free from secretion-droplets. These presently appear in ways characteristic of different glands, and increasing in number and size give to each gland-cell its characteristic histological appearance (fig. 2). Finally, in case of holocrine glands, the cell gorged with secretion is extruded bodily, while in case of merocrine glands only its secreted contents, either in part or in whole, are expelled. The cell in the latter case then resumes its secretory synthesis. Thus the cell passes through a "cycle," which obviously may or may not be repeated (fig. 3). As Van Gehuchten ('90) clearly pointed out, the cell in typical cases passes from a condition of "rest" into a state of active secretion, thence to the phase of excretion, and so back to the original "resting" state. Here again physiological terminology disagrees with the facts of morphology, for the physiologist calls that cell at "rest" which is synthesizing its secretion-product, and applies the term "active" only to cells in process of excretion. Fortunately these contradictions are of little importance since the terms "rest" and "active" are in any event cytological misnomers. The relation between secretory activity and the possibility of mitosis in gland-cells has been much discussed, but its consideration falls beyond the scope of this review. As an introduction to the literature, see for example, Peter ('25).

As a matter of fact, the secretory cycle of the individual gland-cell has received little attention, and its exact nature is still in many cases uncertain (see Bowen, '26a). Clearly in holocrine glands the cycle is very definitely marked. Beginning with an "undifferentiated" cell, the secretion-droplets begin gradually to appear, finally filling the cytoplasm, and the cycle closes with the extrusion of the whole cell. There are other cases in which small aggregates of the secretion are in one way or another "budded" off from the cell-periphery. Examples are found among many glands of lipoidal secretion (R. Heidenhain ('83), Nissen ('86), Altmann ('94)); also the phenomenon of "Pfropfbildung" (so named by Schulze ('67)) or "blasenförmige Sekretion" (van Gehuchten ('91) (?), Henschen ('04), Mislawsky ('09), etc.). This may presumably continue for a longer or shorter period, new secretory droplets being constantly synthesized and moved toward the periphery for excretion. Finally, however, it seems certain that the cycle closes with the loss of the cell as a whole. The end-result is the same as in the strictly holocrine gland-cell, but there is interpolated a long period during which the casting off of cellular fragments loaded with secretion is balanced by a continual synthesis of new droplets. There are other cases, as for example the parotid gland of the cat (Altmann, '94; Bowen, '26a), where under normal circumstances the cell seems to produce a batch of secretory droplets which are then "ripened" without any further significant addition to their number. The entire secretory content then seems to be expelled, the remnant of the cell reorganizing for a new cycle. Presumably after an indeterminate series of such cycles, the cell itself is finally lost ("wears out").

There is, accordingly, in many secretory cells an all-or-none type of response. The cell is not normally prepared to excrete any of its contents until the whole is ready. The special cases just noted are variations which in many ways suggest another type of cycle that is of frequent occurrence. In this case (the tear gland, for example) the cells become gorged with secretion and upon stimulation excrete the more peripheral portion, while the synthetic processes continue undisturbed in the more deeply lying part of the cells. The end-result is not unlike that in some of the cases already noted, except that the secretion-products are, as it were, partially washed out of the cell, instead of being budded off in cellular fragments. And in these cases the rhythms in the cycle are not terminated by a clear-cut all-or-none response, such as often occurs in other glands.

THE ORIGIN OF SECRETION-DROPLETS

Having thus traced the development of opinion concerning glandular activity in so far as this can be formulated in cytological terms, we arrive at the conclusion that the problems of glandular cytology center in the origin of an individual secretory droplet. One of the first discussions of this problem in which the true significance of the facts was broadly recognized and clearly formulated is given by M. Heidenhain, in his *Plasma und Zelle* ('07). In the beginning it was considered satisfactory to explain the origin of secretions as due to mucous or fatty degeneration (e.g., Virchow ('57), R. Heidenhain ('68), etc.); or as related in an indefinite way to theories of protoplasmic structure (Schiefferdecker, ('84), Mislawsky and Smirnow ('93), Ver Eecke ('95), Carlier ('96), Hammar ('97), Montgomery ('98), Harrington ('99), Pacaut and Vigier ('06), etc.). During the eighties of the last century, however, attention began to focus more sharply on this essential problem of secretory origins. In the intervening half-century literally scores of conflicting cytological explanations of secretory synthesis have been presented. In the remaining portion of this review, I wish to discuss the general results of these investigations and to attempt some critical estimate of our present knowledge. The measure of the probability of a particular interpretation must obviously be the ability of a set of observations to account for the origin of a single, individual, secretory droplet.

For convenience in handling the vast mass of accumulated material, I shall begin the discussion with those views which find a center for secretory activity in the nucleus; and thence I shall pass over into the cytoplasmic aspects of the problem.

THE RÔLE OF THE NUCLEUS IN SECRETION

> Daraus ist die eigenthümliche Ausbildung des Kernes in diesen kolossalen Zellen [der Raupenspinngefässe] zu erklären. Der Kern verästelt sich durch die Zelle hindurch, um überall seinen Einfluss geltend zu machen und die Sekretion zu vermitteln.
>
> (Meckel, 1846.)

> Dies spricht dafür, dass der Kern vor allem für die secretorische Function der Zelle eine besondere Bedeutung hat.
>
> (Korschelt, 1889.)

> Les recherches minutieuses faites sur cette question prouvent que le processus sécrétoire du noyau, que la participation du noyau à la sécrétion protoplasmique peut se faire suivant un mode assez variable et d'une façon plus ou moins évidente.
>
> (Maziarski, 1910.)

One of the most widespread and deep-seated beliefs in zoölogy seems to be that the nucleus is the source of enzymes and secretions generally. It is argued, on grounds either of theoretical necessity or direct observation, that materials pass from nucleus to cytoplasm, there to become secretions. This theory requires, as a fundamental basis, the transfer of material from cytoplasm to nucleus and vice versa. That such exchanges must occur in any event seems rather obvious and the enormous growth of the nucleus during development of an egg, or during the reconstruction-stages following mitosis, is ample evidence that materials must pass into the nucleus from the surrounding cytoplasm. It is generally agreed that such contributions are made through the nuclear membrane in soluble form, and not by the penetration of formed material, although some exceptional accounts in the older literature are cited by Korschelt ('89); (see also Montgomery ('98)). With respect to the passage of substances from nucleus into cytoplasm, there is much disagreement, as noted later in more detail, but demonstrative evidence of the passage of material from the nucleus, as indicated indubitably by decrease in nuclear size, is rather scanty. Nevertheless the fact should not be lost sight of that during mitosis the bulk of the nuclear content is cast out directly into the cytoplasm, and such being the case, there seems no adequate reason why nuclear emissions might not also occur during the interkinetic phase. (See also, for example, Korschelt ('89), and the more extended discussion on page 316.)

The view that the nucleus is the primary agent in cellular synthesis was clearly formulated by Claude Bernard in 1878, although the idea had been variously expressed by his predecessors. Evidence for this view is now frequently based upon experiments in subdividing Protozoa, such as were first made by Nussbaum in 1884 and subsequently substantiated by Gruber, Balbiani, Hofer, and many later workers, extended discussion of which may be found in Nussbaum ('86), Henneguy ('96), page 451, Wilson ('28), page 657, and especially Sokoloff ('24). The results of Wallerian degeneration in nerve fibers, and changes in nuclear appearance in gland cells, and the work of Spitzer ('97), Loeb ('99), and Lillie ('02) on the nucleus as an oxidative center—a view now largely abandoned—have also been held to confirm the view that the nucleus plays the decisive rôle in operations of synthetic metabolism. That the nucleus coöperates in cellular synthesis would hardly be denied by anyone, but the prevailing opinion as to the importance of the nucleus seems to have been emphasized beyond the point justified by the facts. That a non-nucleated cell-fragment will not behave like a nucleated piece might be guessed in advance from modern conceptions of the cell as a system. But it does not follow that, because the behavior of two fragments can be correlated with their nuclear content, the nucleus must perforce be the all-important element of the cell. We have rather proved that the nucleus is a necessary part of the cell and that when the cellular system is upset by its removal, disaster is the only possible result. It is at least possible that if some of the cytoplasmic components could be removed, the remainder of the cell, even though nucleated, would never effect a complete recovery. Indeed exactly this result is reported by van Wisselingh ('08), who, by centrifuging filaments of *Spirogyra*, obtained fragments with a nucleus but very little of the chromatophore. Such cells could not effect their own reconstruction even though the nucleus was present. It is interesting also to recall Whitman's ('88) views, which sound almost contemporary. According to Whitman, nucleus and cytoplasm form a physiological unit, which must disappear once the unity is destroyed—that is, when nucleus and cytoplasm are separated. Quoting Whitman (p. 37–8): "Allowing that regeneration is impossible in the absence of a nucleus, that is no proof that the nucleus is the sole seat of regenerative power, nor is it proof that the nucleus is a more important factor than the cytoplasm." (Compare also Verworn ('91).)

Such being our uncertain position in respect to the general possibilities of the nuclear rôle in secretion, it is next in order to examine the actual result of cytological investigation of the nucleus in gland-cells. There are, in the first place, indices of nuclear coöperation in secretion which might supply valid evidence of activity without giving any specific indication of the exact part played by the nucleus. Such indices involve the assumption that material, elaborated within the nucleus in soluble (and therefore invisible) form, passes through the nuclear membrane by diffusion, to become in the cytoplasm a part of some visible secretory product. In the second place, it is conceivable that the nucleus might produce formed materials which would be extruded bodily, or else passed out by diffusion after prior solution (compare, for example, Macallum ('91), Maziarski ('10)). In one or both of these possibilities we must look for evidence of nuclear coöperation in secretion.

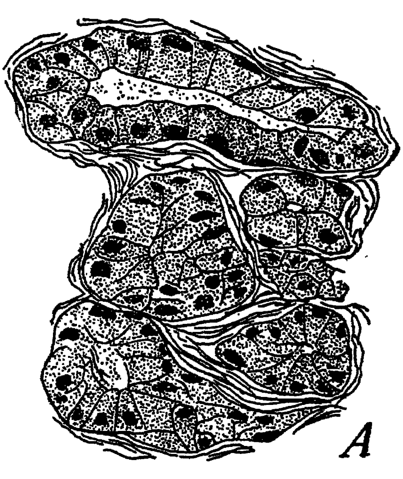

Fig. 3. Changes in Appearance of Gland-cells Before and after Excretion—as Seen by Earlier Workers (Lachrymal Gland)

A, before excretion—cells large and clear, with flattened, angular nuclei; *B*, after excretion—cells smaller, more granular, with large rounded nuclei which occupy a more central position in the cells. From Reichel, 1880.

Shape, Size, Position, and Staining Capacity as Evidences of Nuclear Activity in Secretion

> Mit der Betheiligung des Kernes an der Thätigkeit der Zelle ist eine Veränderung seiner Structur verbunden.
>
> (Korschelt, 1889.)

> Wir kommen also im ganzen darauf zurück, dass eine direkte Mitbeteiligung des Kernes an der Sekretion oder der Erzeugung der Granula bisher nicht mit Sicherheit nachgewiesen wurde; dagegen räumen wir ein sekundäres Eingreifen des Kernes auf Grund seiner regenerativen Potenzen ohne weiteres ein und hiermit mögen eventuell gelegentlich auch Veränderungen des Kernes in Bezug auf Form, Volumen, Wechsel der Färbbarkeit etc. Hand in Hand gehen.
>
> (M. Heidenhain, 1907.)

The first clear-cut accounts of changes in nuclear appearance correlated with the secretory cycle were given by R. Heidenhain ('66, '68, etc.) and his pupils, particularly Lavdovsky ('76). Thus, in the parotid gland of the rabbit, Heidenhain found the nuclei, in cells loaded with secretion, to be irregular (jagged) in outline with no nucleoli visible, while in early phases the nuclei appeared rounded-out and nucleoli could be discerned. Similarly, in the orbital gland of the dog, Lavdovsky found the nuclei flattened against the basal wall of the cell, while after excretion, they rounded-up and moved into a more central position. Like changes in gland-cells of many kinds were noted by many later workers (fig. 3) and one case of a branched nucleus, very rare among vertebrates but not unusual in invertebrates (cf. p. 313), is cited by Carnoy ('84) in *Chelone*. Schmidt ('82) summarizes these changes, noting the differences in nuclear shape, size, position and staining capacity before and after excretion. The older literature is well reviewed by Korschelt ('89). Cases of variation in the chromaticity and other general morphological features of the nucleus in more recent literature are noted by Nicolas ('91), Carlier ('99), Henry ('00), Regaud and Policard ('01), Regaud ('02), Launoy ('03a), Fuchs ('04), Hoven ('12), Eklöf ('14), Jirešova ('18), Dolley ('25), Benoit ('26), Urasov ('27, '28), etc. Noll ('01) observes that some of these changes are discernible only after fixation and staining. An excellent tabulation of the older results is given by Mathews ('99); and later summaries by Garnier ('00a), Launoy ('03b), Laguesse ('05–6), and Benoit ('26).

It should be noted that these conclusions have been drawn from the study of vertebrate gland-cells, where nuclear changes during the secretory cycle are at most relatively inconspicuous, and there is indeed no agreement that such changes as do occur are necessarily indicative of nuclear participation in secretion. Korschelt ('89) in particular was disposed to accept the nuclear changes as circumstantial evidence of nuclear complicity in secretion, and a similar view has been taken by many writers down to the present time (e.g., Launoy, '03a; Jirešova, '18; Conklin, '24; Benoit, '26, etc.). Others, notably Nussbaum ('82), have held that these changes are due primarily to compression of the nucleus by the accumulating secretory granules. In other words, the changes in appearance are largely of mechanical origin, and tell us little about the actual function of the nucleus in a gland-cell (Kolossow, '98; M. Heidenhain, '07; Bowen, '26; and also List, '86); are merely evidence of the metabolic activities common to all cells (Gurwitsch, '04); are indications of "regenerative" activity (M. Heidenhain, '07); or represent regressive metamorphoses (Hermann, '88) or degeneration (Henry, '00). Mathews ('99) could find no periodicity in chromatic changes of the nucleus, while Garnier ('00) concluded that the changes followed no recognizable rule, and Launoy ('03a) interprets changes in nuclear size and position as "passive."

In invertebrate gland-cells, the nuclear behavior is often very remarkable, particularly with respect to the shape of the nucleus and to some extent its stainability. The best known examples are the spinning glands of insects, especially Lepidoptera. In these cells the nuclei are at first sensibly ovoidal, but subsequently they become extraordinarily branched so that each nucleus extends itself throughout the cell (fig. 4). These amazing nuclei, discovered by Meckel in 1846, have been studied by many workers (bibliographies in Korschelt ('89), Gilson ('90), Maziarski ('11), Kinney ('26), etc.). Even more remarkable are the nuclei in the spinning glands of *Cladius* (Korschelt, '89), and in the appendage glands of *Phronimella* (Mayer, '78). Other noteworthy cases are the nuclei in certain genital glands of *Branchipus* and the double-cells in the egg-follicle-wall of *Nepa* described by Korschelt ('89); also in the spinning glands of *Platyphylax* (Marshall and Vorhies, '06), and in isopod gland-cells by Conklin ('97) and Prenant ('97). Here the nuclei send out branching "pseudopodia" which are developed only on the side of the nucleus directed toward the accumulating secretion. Still other examples of abnormal nuclear structure in invertebrates are cited by Korschelt ('89). Changes in the mere position of the nucleus are not conspicuous even in invertebrates (Korschelt, '89; Holz, '09). Variations in staining capacity are perhaps more suggestive than in vertebrates, but are rarely of striking nature. An extended series of observations (and discussion) bearing on the morphological changes in nuclei of isopod gland-cells is given by Maziarski ('10), and of other invertebrate gland-cells by Issakowitsch ('10), Maziarski ('11), Jörgensen ('13), Lutz ('21), Frankenberger ('23), Roskin ('25), and Millot ('26). Nevertheless, in spite of the remarkable nuclear conditions which certainly occur in many invertebrate gland-cells, it should be carefully noted that there are certain facts which may well cause us to hesitate in assigning over much importance to these "evidences" of nuclear participation in secretion. Thus Van Gehuchten ('90), in digestive cells of *Ptychoptera*, could find no evidences whatever of nuclear change; Krüger ('23) found no changes in reaction to basic dyes in the

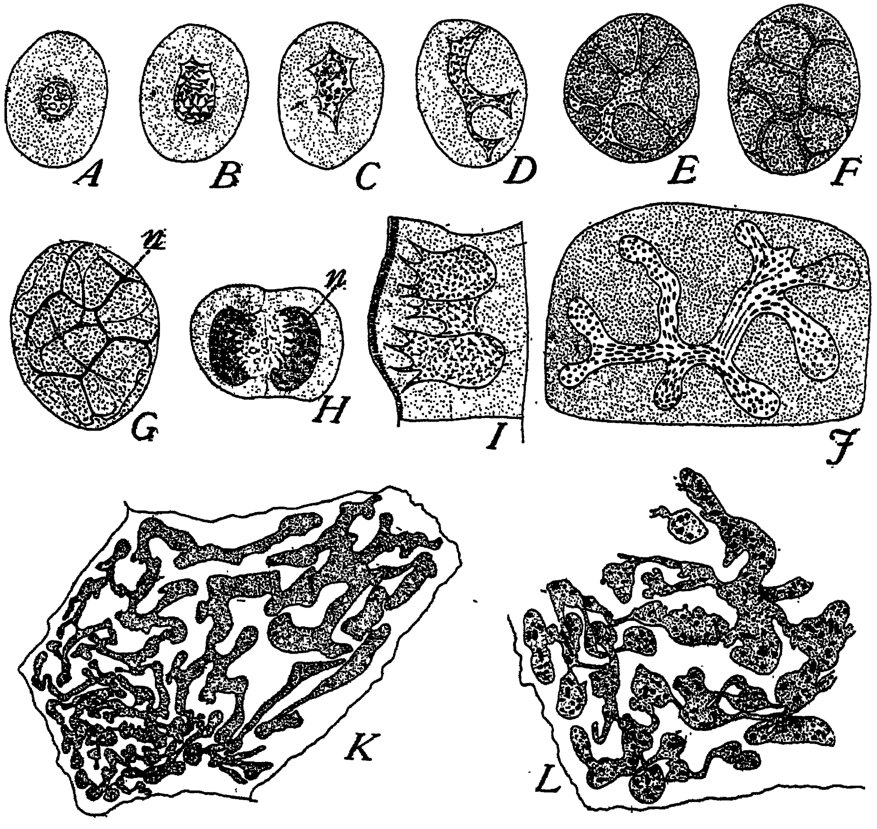

FIG. 4. MORPHOLOGICAL CHANGES IN THE NUCLEI OF ARTHROPOD GLAND-CELLS

A to *G*, in spinning glands of the larva of *Cladius*; *H*, "double-cell" gland in the genital apparatus of *Branchipus*; *I*, *J*, profile and plane view respectively of spinning gland-cells in the fresh condition, from the butterflies *Vanessa* and *Pieris*; from Korschelt, 1889.—K, a cell from the spinning glands of the larva of *Platyphylax* (nucleus stippled), and *L*, detail of a portion (lower left corner) of the nucleus of the cell in K; from Marshall and Vorhies, 1906. *n*, nucleus.

cement-glands of *Scalpellum;* while Gilson ('94) and Conklin ('97) find evidences that "nuclear pseudopodia" are merely the result of the mechanical indentation of the nuclear wall by the accumulating secretory droplets, and Murlin ('02) later concluded that they were fixation-effects, being entirely lacking in the living cell. Millot ('26), in certain glands in spiders, found no changes in nuclear shape. Further, Marshall and Vorhies ('06) found that the branching nucleus in the spinning gland-cells of *Platyphylax* showed no variations in shape corresponding to differences in secretory activity induced by experimental means. Finally, Seeliger ('00) has described in the muscle cells of the tail of appendicularians a most astonishing branched nucleus, where presumably no special secretory activity is involved.

Beyond the fact that the nucleus varies slightly in size, being smaller in cells gorged with secretion (according to R. Heidenhain and his pupils), conspicuous differences in volume are very unusual. Conklin ('24) reports that in *Crepidula* the nuclear volume in a liver-cell filled with secretion is only one-fourth as great as in a cell without secretion. This is taken to prove that during secretory synthesis, substances pass from nucleus to cytoplasm. Additional evidence is cited by Lukjanoff ('98), Phisalix ('00), and Schreiner ('18); but Launoy ('03a) considers that size-changes are merely passive.

On the basis of all these changes during a secretory cycle, the conclusion has been repeatedly drawn that the nucleus partakes in an important way in secretory activity. This view was carefully developed by Korschelt in 1889, and it must be said that little of a substantial nature has since been added. So far as vertebrate tissues are concerned, the argument for a direct connection of the nucleus with secretory synthesis is not particularly convincing. Too often the nucleus behaves outwardly as though it were unconcerned with the changes occurring in the cytoplasm. Certainly nuclear phenomena sufficiently marked to arrest attention are uncommon. Among invertebrates, however, even allowing for the apparent contradictions mentioned above, the remarkable nuclear changes, particularly in shape, are difficult to explain except in terms of secretory coöperation. In so far, therefore, as the argument rests upon the superficial appearance of the nucleus, it might be concluded that the facts warrant a belief that nucleus and cytoplasm in some way coöperate in secretory synthesis, the necessary exchanges being invisible to the cytologist because their material substratum is in soluble form (compare Lutz ('21), Yamanouchi ('22), Dolley ('25), Benoit ('26), Bowen ('26d), Ma ('28), Jacobs ('28), and many others). Earlier accounts often interpreted the secretory rôle of the nucleus in some such simple and rather intangible manner. In the later literature, an attempt is occasionally made to interpret the phenomena in terms of the extrusion from the nucleus of soluble "prozymogen" (Macallum, '91), of chromatic material in soluble form (Henry, '00; Launoy, '03b; Goldschmidt, '05; Jörgensen, '13; Benoit, '26), of nuclear sap (Launoy, '03c), etc.,—attempts of purely speculative character. (See also the section on the Chromidia, page 321.)

In a few instances, especially in the older literature, secretions have been directly derived by a presumed transformation of the entire nucleus. Such extraordinary accounts now seem in the highest degree improbable. For examples, see Calmels ('82), Nissen ('86), Steinhaus ('88), Ver Eecke ('95), Michaelis ('98), Limon ('02), and others. In many cases where such transformations have been described, the cells are said to be binucleate.

Thus, one nucleus can be directly transformed into secretion-products, while the other one remains behind to continue the cycle. Binucleate conditions have been noted in many glands, for example, Calmels ('82), Frenzel ('85), Steinhaus ('88), Van der Stricht ('93), Harrington ('99), Aigner ('00), Limon ('02), Brinkmann ('12), Schiefferdecker ('17), and Parat ('28). Further, Gilson ('90) has reported silk-secretion within the nuclei of the lepidopteran spinning gland, and Browicz ('05) believed that he had demonstrated the active share of the nucleus in secretion through his observation of bilirubin within the nucleus of liver cells. In holocrine gland-cells, the nucleus is of course included in the excretory product, but this phenomenon obviously belongs in a different category.

The Nucleus as a Seat of Production of Visible Secretory Materials

> Le noyau joue un rôle important dans les processus sécrétoires; il participe directement à la formation du produit de sécrétion. C'est la substance nucléolaire qui donne le matériel pour les processus sécrétoires.
>
> (Maziarski, 1911.)

> Es findet kein Austritt der "Chromidien" aus dem Kerne statt, und man kann auch keine Beziehung derselben zur Kernmembran feststellen.
>
> (Kulmatycki, 1922.)

The real argument for the participation of the nucleus in secretion is, however, usually based on evidence less circumstantial in nature. The view has been widely expressed that the nucleus produces secretory materials in visible form, which are then extruded bodily (but sometimes only after solution) into the cytoplasm. General reviews of the evidence supposedly favoring such an opinion are given by Galeotti ('95), Henry ('00), Vigier ('00b), Launoy ('03b), Goldschmidt ('05), Prenant ('05), Laguesse ('05–6), Maziarski ('10), Krüger ('23), Benoit ('26), and Millot ('26). The first account of this phenomenon is that of Ogata ('83) in the pancreas, followed by many subsequent observations of similar phenomena. The results may be arranged in three groups according to the mode of origin of the secretion:—

1. Origin from nuclear substance of indeterminate identification.

2. Origin directly or indirectly from nucleoli.

3. Origin from the chromatin (chromidia, etc.)

1. The origin from the nucleus (the term being here used in a general sense) of secretory droplets, or of formed materials which precede them, has been occasionally described, although the results present no agreement in details and have rightfully found no acceptance. Thus Galeotti ('95, '97) describes in various amphibian glands the appearance within the nucleus of small granules which migrate into the cytoplasm and become secretory granules. Somewhat similar examples are supplied by Engel ('09) and Roskin ('25). Hammar ('97) believed that the granules arose from the nuclear sap, while Ikeda ('06) and Ziegler ('27) are entirely indefinite. Holz ('09) and more especially Greschik ('15), in the intestinal epithelium of *Nematus*, assert that all the nuclear constituents contribute to the formation of a great secretory vacuole which fills a large part of the original nucleus and is finally extruded from the cell. Here also may be noted the "nucléo-rouge" bodies recently described by Dehorne and Hosselet ('28a), which emerge from the nucleus and are said to give rise eventually to chondriosomes ('28b).

2. The nuclear component most frequently described as the source of secretory materials, is, however, the true nucleolus or plasmosome, of which one or many constantly occur in gland-cell nuclei.

Our ignorance of the real significance of the nucleolus is axiomatic, although many workers have made more or less hypothetical suggestions. Some of the work (cf. vom Rath ('95), Saguchi ('20a), Krüger ('23)) on the nucleolus as a structure supposedly associated with secretory phenomena, seems to have found its source in the so-called nuclear secretion-hypothesis of nucleolar function—a view associated particularly with the name of Haecker. Nevertheless, the theories which attempted to define the functional significance of the nucleolus in generalized terms seem to have had little influence on workers interested primarily in gland-cells, and conversely the results obtained by students of secretory problems have never been accepted as decisive indication of the function of nucleoli in general. In secretion-studies, the variations in described behavior of nucleoli are extraordinarily diverse. Not only do the nucleoli vary in the supposed manner of their participation in secretory synthesis, but their origin, their mode of transportation across the nuclear boundary, and their behavior in the cytoplasm have been described in every possible way. Extended reviews of the nucleolar problems in gland-cells are given by Montgomery ('98), Vigier ('00b), Launoy ('03b), Prenant ('05), Maziarski ('11), Ludford ('22), Benoit ('26), and Millot ('26); and a paper by Hoffman ('02), dealing more particularly with the egg, and the classical paper by Korschelt ('89) contain much of interest.

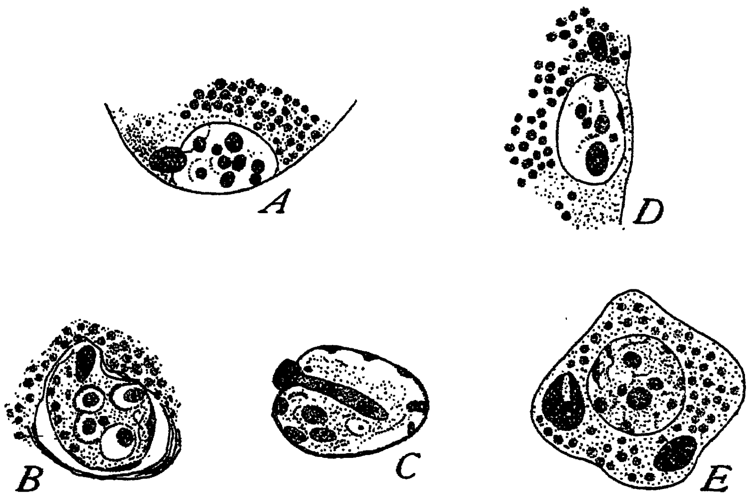

Fig. 5. Various Steps in the Supposed Extrusion into the Cytoplasm of a Nucleolus, in the Pancreas of Salamanders

A portion only of the cell is shown in *A*, *B*, and *D*; in *C*, the nucleus alone, still in contact with an extruded nucleolus. Secretory granules in the cytoplasm are stippled; nucleoli, solid black. From Ogata, 1883.

All of the accounts of nucleolar activity in secretion go back to the work of Ogata ('83), who first described the emergence of the nucleolus (fig. 5) (pancreas-cells), and its subsequent transformation into a cell loaded with secretion products ("Zellerneuerung"). Since this work, which in some respects is obviously incorrect, the bodily extrusion of nucleoli or their products from nucleus into cytoplasm, where in one way or another they participate in the formation of secretion-granules, has been repeatedly described.

Examples are vom Rath ('95), Henry ('00), Vigier ('00a, '01), Maximow ('01), Launoy ('03b), Maziarski ('11), Nakahara ('17), Schreiner ('16, '18), Saguchi ('20a, b), Skowron ('22), Krüger ('23), Ludford ('25a), Kinney ('26), Millot ('26), Noel and Paillot ('27), Jacobs ('28), Beams and Wu ('29). Many additional examples, especially between the years 1885 and 1900, might be cited, in which the extruded nucleolus is said to become the so-called nebenkern (parasome, etc.). These have, however, for the most part been referred to the discussion of the nebenkern on page 320. Occasionally the nucleolar products are said to undergo dissolution within the nucleus, the emission and further fate of this material being then beyond the reach of all but speculative explanation (e.g., Launoy ('03b, c), Benoit ('26)).

These examples cover many kinds of glands from both vertebrates and invertebrates. The story they tell is in essence the same. During the secretory cycle the nucleoli enter upon a phase of growth and in many cases multiplication, often accompanied by amoeboid changes in shape, differentiation into materials with special staining characteristics, and many other structural modifications. Most workers have considered the nucleoli in gland-cells simply as plasmosomes; but a few (e.g., Vigier ('01), Guieysse ('07), Saguchi ('20a), Noel and Paillot ('27)) derive them specifically from chromatin. According to Saguchi ('20b) certain secretory products come from the nucleolini—a special part of the nucleolus. This material, however produced, is transported to the cytoplasm where it usually undergoes modification or union with cytoplasmic materials before the definitive secretion is formed (most of the cases cited above); or in rare cases may be ready for immediate excretion (Henry, '00; Maziarski, '11). The most remarkable case is perhaps that of the silk-glands of insects described in extraordinary manner by Maziarski ('11), and in part corroborated by later workers (cf. Nakahara ('17), Kinney ('26), Noel and Paillot ('27), Dehorne and Hosselet ('28a)). According to Maziarski, the branching nuclei (fig. 4) contain a host of nucleoli, which probably multiply by fission (Vorhies, '08; Maziarski, '11), thus maintaining the supply. These nucleoli are said to be extruded from the nucleus in several ways according to the intensity of secretory activity. They become individually enclosed in vacuoles, usually while still within the nucleus, and the secretory droplets thus constituted are excreted without any cytoplasmic contribution.

Without attempting for the moment to examine critically the phenomenon of nucleolar extrusion, it may be pointed out that Maziarski's figures are so compellingly clear that one finds it hard to see any possibility of mistake. In short, the secretion-problem seems indubitably settled. Nevertheless, Nakahara ('17) could not find in *Pieris* the striking phases of activity described by Maziarski, and although he found nucleolar extrusions, his figures are decidedly less concrete. Subsequently, Kinney ('26), in *Hyphantria*, finds evidences of nucleolar extrusion only in similarity of staining reaction between the secretory granules in the cytoplasm and the intra-nuclear nucleoli. But she adds, perhaps significantly, that the number of nucleoli is not reduced during secretory activity, as one might perhaps expect. Finally, Yamanouchi ('22), in the silkworm, categorically denies the occurrence of nucleolar extrusion. It may also be noted that Korschelt ('96) and Meves ('97) fail to mention nucleolar extrusions (similarly, Marshall and Vorhies ('06), and Vorhies ('08)). If such phenomena are at all conspicuous or demonstrative, it is more than strange that two such observers failed to note them. Thus, in a case which may be chosen as one of the best possible examples of nucleolar participation in secretion, the actual facts turn out to be surprisingly equivocal.

Conclusions as to the secretory rôle of the nucleolus are further rendered doubtful by the lack of uniform or satisfactory descriptions of how nucleolar material gets through the nuclear membrane. Some authors have described a direct perforation of the nuclear wall (Melissinos and Nicolaides ('90), Ver Eecke ('95), Carlier ('96, '99), Vigier ('01), Launoy ('03b), Ferrata ('06), Walker and Embleton ('08), Benoit ('21), Skowron ('22), Ludford ('25a), Jacobs ('28)), the membrane sometimes presenting visible evidences of an actual tear or rupture, and sometimes not. According to Ogata ('83) the nucleolus may "bore" through the membrane; Krüger ('23) believes that the nucleolus exerts a solvent action on the nuclear membrane at the point of contact; nuclear contractions assist in the expulsion of the nucleolus according to Maziarski ('11) and Montgomery ('98); and the nucleus may be drawn out into elongate processes, from the tips of which the nucleoli escape (Petersen ('07), Maziarski ('11); compare also Engel ('09)). There are also a few cases in which definite openings in the nuclear wall seem to occur (Vigier ('00a)) (compare also Galeotti ('95) and the "Karyopyle" of Ikeda ('06)). Other workers find a sort of budding phenomenon (Platner ('89), Laguesse ('24), Ludford ('25a)); others report a thinning of the nuclear membrane and subsequent passage of (colloidal?) materials without leaving any trace of their exit (Lukjanow ('88), Guieysse ('07); while still others describe an apparent disappearance of the membrane at the place of discharge (Ogata ('83), Henry ('00), Holmgren ('02), Maziarski ('11), Nakahara ('17), Noel and Paillot ('27)). According to Vigier ('00b), a large vacuole may arise in association with the nucleolus, within which the secretory granules appear, escaping thence by nuclear rupture, and Urasov ('28) describes the direct transformation of a nucleolus into a great intranuclear vacuole in which the secretory droplets develop. Other cases of this kind are reviewed by Urasov ('28).

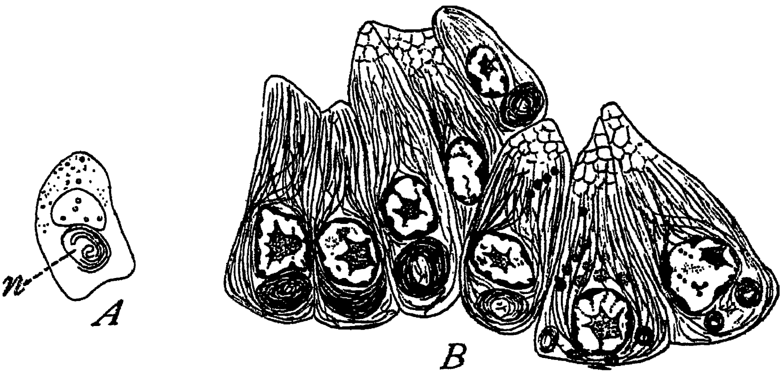

Fig. 6. The Nebenkern in Gland-cells

A, original figure from the pancreas of *Salamandra*, from Nussbaum, 1882; *B*, in the pancreas of the frog, from Mathews, 1899. *n*, nebenkern.

Before concluding the subject of nucleolar participation in secretion, the so-called "nebenkern" (fig. 6) of some gland-cells should be mentioned. These nebenkern structures have been frequently associated with the ergastoplasm, which is separately considered in Section II. It is to be clearly understood that this structure in gland-cells (particularly the pancreas) has nothing whatever to do with structures of similar name in pulmonate germ-cells and in insect-spermatids. The nebenkern (parasome, paranucleus, accessory nucleus, etc.) in a gland-cell is a mass, often of fibrillar structure, the origin and meaning of which are still much in dispute. It was first described in gland-cells by Nussbaum ('82), who adopted for it the term "Nebenkern" (fig. 6*A*), which had already been introduced by Gaule ('81). Nussbaum observed that the development of the nebenkern was related to the phase of the secretory cycle in which a given cell happened to be, and like observations were made by many later workers. Cells engaged in active synthesis of secretory droplets were found to contain one or more large nebenkerns, while in cells loaded with secretion the nebenkern might be absent.

The history of this structure as a factor in secretory synthesis really begins with Ogata ('83), who first described its origin from a nucleolus which had migrated out of the nucleus. Its subsequent history was handled by Ogata in rather fantastic fashion (see also Ver Eecke ('95)), but the essential point here is his belief that the nebenkern is in one way or another the material basis of new secretory granules. For the next twenty years the literature of glandular phenomena was dominated by the nebenkern-conception. Since 1900, however, the importance of the nebenkern in gland-cells has received less and less emphasis, and the most recent studies scarcely mention it. The great interest formerly felt in the nebenkern produced numerous detailed and exhaustive reviews. To these reference should be made for a more adequate discussion than the present status of the matter seems to call for in this review. See, for example, Eberth and Müller ('92), Galeotti ('95), Henneguy ('97), Prenant ('98–'99), Mathews ('99), Garnier ('00a), Oppel ('00), Launoy ('03b), Laguesse ('05–'06, '24), Babkin, Rubaschkin and Sawitsch ('09), and Champy ('11). Following Ogata, however, quite a number of workers described the origin of the nebenkern or parasome by the direct extrusion of a nucleolus, followed usually by fragmentation or some more indirect change into secretory droplets (e.g., Melissinos and Nicolaides ('90), Galeotti ('95), Ver Eecke ('95), Vigier ('01), Maximow ('01), Guieysse ('07)). Platner ('89) flatly denied the occurrence of such a phenomenon, and stated that nucleoli only "traversed" the nuclear membrane in *paraffin sections* (!)—a contention in which he was later sustained by Babkin, Rubaschkin and Sawitsch ('09). Platner ('89) himself and Laguesse ('93, etc.; '24) held that the nucleolus was budded off in a lobe of the nucleus, but never actually penetrated the nuclear membrane. Others have traced the nebenkern structures to the cytoplasmic reticulum, ergastoplasm, etc., sometimes in combination with nuclear or other material (cf. Lukjanow ('87), Hammar ('97), Garnier ('00b), Babkin, Rubaschkin and Sawitsch ('09), Benoit ('26)). Garnier ('00a) in one case described the nebenkern as arising by transformation of an entire nucleus; and M. Heidenhain ('90) dismissed the nebenkern structures as products of degeneration. Pensa ('19) has recently given a discussion of these structures in terms of the physical state of the protoplasm in gland-cells.

On the whole, it must be confessed that the subject is in a very chaotic condition, with little hope of immediate betterment. Certainly in many gland-cells there is no nebenkern present at any stage and there is much reason to believe that its appearance in fixed preparations was frequently due to faulty fixation (Morelle, '27a). Recent workers have been rather inclined to classify the nebenkern with the ill-starred ergastoplasm (see Section II), and to assign to it a minor place in the economy of a gland-cell (Benoit, '26). Some even of the older workers questioned whether it had any direct connection with the formation of secretory granules (Eberth and Müller, '92). It is my personal opinion that in the present state of our knowledge further study of the nebenkern structures can hardly be expected to shed much light on the more immediate problems of glandular cytology.

3. There remains the possibility that secretory granules, or their intermediate products, may be derived from the so-called nuclear reticulum—the linin and chromatin. Most of the work in this direction has been along the general lines of the well-known chromidial hypothesis of Goldschmidt ('05). According to this view, cytoplasmic differentiation is traceable to "trophochromatin" extruded (either directly or by osmosis) from the nucleus. The theory was not particularly developed by Goldschmidt in gland-cells, and he merely connected his general view with various structures previously described in gland-cells—particularly the ergastoplasm (see Section II). Other students of the chromidia were interested particularly in the egg, and gave little attention to gland-cells. The most extended paper is that of Erhard ('10) (see also Popoff ('10), Issakowitsch ('10), Dolley ('25)) who described nuclear extrusions which participated in various ways in the production of secretory granules. Older workers who connected the chromatin with secretion are Macallum ('91), Henry ('00), Conte and Vaney ('02), Launoy ('03b), Fuchs ('04), Carlier ('05), Nussbaum and Kulczycki ('06), and particularly Phisalix ('00); and more recently Maziarski ('11), Winiwarter ('25) and Benoit ('26). In some of these cases the secretion was described as arising within the nucleus directly from chromatin.

However, no very clear picture has emerged of how chromatin arrives at the end-stage of a secretory droplet, and accounts of different authors rarely present points of striking similarity. The present status of the chromidial hypothesis (together with a useful review of the literature) has recently been examined by Kulmatycki ('22), who comes to the conclusion that the chromidia (in *Ascaris* at least) are deformed mitochondria, and are not derived from nuclear extrusions. Jörgensen ('13) has likewise denied the extrusion of formed chromidia, and concludes that there is little evidence that the nucleus plays any definite part in secretion. It now seems clear that the attempt to classify all the formed materials in the cytoplasm as chromidia was a mistake, and to this extent interpretations of the chromidia in gland-cells are more properly referred to the special theories connected with the ergastoplasm, chondriosomes, etc. Similarly, accounts of secretion based on nuclear extrusions of very special kinds, may be considered in connection with the intermediate cytoplasmic products with which they were associated; as, for example, the views of Schreiner ('16, '18), Saguchi ('20a), and Laguesse ('24), Section II; and also the relation of the ergastoplasm to the nucleus, Section II; etc.

A Critique of Nuclear Function in Secretion

Daher leugnen wir im allgemeinen die unmittelbare Beteiligung des Kernes an der sekretorischen

Funktion und der Genese der Granula, schreiben ihm vielmehr ein regeneratives Vermögen zu.

(M. Heidenhain, 1907.)

Die Sekretion ist eine Folge der vereinten Tätigkeit von Kern und Protoplasma.

(Lutz, 1921.)

From this review, fragmentary though it necessarily is, it must be evident that attempts to derive secretions from the nucleus have been more characterized by their differences than their similarities. Workers, even on the same material, seem unable to corroborate details of what, one might suppose, would be very conspicuous features. This failure to reach some agreement could perhaps be cared for by the explanation that in different gland-cells a common method of secretion is not to be expected. But to many such an interpretation would seem quite impossible, and it would be more in accord with our views of organic unity to anticipate that phenomena occurring in one secretory cell would appear, though perhaps with varying degrees of visible emphasis, in all secretory cells. To what extent either of these points of view is upheld by available facts may perhaps be clarified by a brief analysis of the accumulated theories.

It will, I judge, be agreed that the bizarre accounts so common in the eighties and nineties must simply be traced to inadequate technique and outright errors of observation and interpretation. Similarly, practically no one now expects to find a solution in the behavior of the chromatin, particularly its supposed extrusion through the nuclear membrane. The reasonable probabilities there narrow down to the possibility of nucleolar activity, or to a somewhat intangible, at best ill-defined, coöperation of nucleus with cytoplasm.

With respect to the nucleolar theories the matter obviously turns on whether nucleoli or their products ever traverse the nuclear membrane. To this question endless contradictory answers have been given, but it is significant that those who uphold nucleolar extrusion have not usually stated that they actually saw the essential stages of transfer. Authors who claim, however, to have observed this phenomenon in fixed preparations of gland cells are Ogata ('83), Montgomery ('98), Carlier ('99), Vigier ('00a), Ferrata ('06); refer also to Ludford ('25c). Nucleoli have very often been identified in the cytoplasm on the mere basis of staining capacity. Clearly, such "proofs" are valueless—as much practical experience has shown. Too frequently authors deal with nucleolar migration into the cytoplasm as though it were a "well-known fact," or at most a matter of slight importance. Actually, however, it is exactly this point which is in great present need of being adequately demonstrated or finally disproved. We may hope eventually to get decisive light on this problem through studies which have for their raison d'être exactly the examination of this critical point with no regard for its possible significance. Observation of living cells would be most convincing, even though the conditions of such studies might not be entirely acceptable as normal. On this point, however, very few observations have been made and they would in any event be difficult. Leydig ('88) reported seeing the extrusion of nucleolar derivatives in the egg of *Theridium*, and Ludford ('25c) has recently reported on nucleolar movements in rat fibroblasts grown in tissue cultures, though he was unable to see any actual extrusion of nucleolar material as such. He did, however, observe the appearance of a cytoplasmic vacuole touching the nuclear membrane at its point of internal contact with the nucleolus. He interpreted this as probably a stage in the extrusion of nucleolar material (see also Dehorne and Hosselet ('28a)). These observations obviously afford a rather tenuous basis for such wholesale nucleolar extrusion as existing accounts in gland-cells require. I think, however, that the extrusion of nucleolar matter may well be a fact in gland-cells, developing eggs, etc., without in any way throwing new light on nucleo-cytoplasmic interchanges or secretory activity. For during mitosis, the casting out into the cytoplasm of nucleolar material at the close of the prophase is of regular occurrence, although this material has not been shown to do anything beyond gradually merging with the cytoplasm. It seems to me at least conceivable that if the nucleus can thus rid itself of nucleolar material at one phase of its cycle, it might do the same thing at other times when for some reason the nucleolar situation required readjustment. Thus the mere extrusion of nucleolar products during the interphase may be quite devoid of significance so far as the direct origin of secretory materials is concerned. In some such way have Walker and Tozer ('09) viewed nucleolar extrusions, holding that this phenomenon is common to all cells but is particularly emphasized where active metabolic processes are taking place with mitosis occurring only at rare intervals, if at all. Thus the nucleus may adjust itself to the situation by a process which is ordinarily reserved for the mitotic phase, and no more in the one case than in the other is there any reason to suppose that the material cast out has any direct connection with secretory synthesis (see also Jörgensen ('08), Benoit ('26)). Further, a number of authors, while admitting the validity of nucleolar extrusion, have denied that the material thus transferred to the cytoplasm has any visible connection with secretion. On the contrary the extruded nucleoli seem to break up and disappear (Carlier ('96, '99, '05), Petersen ('07), Walker and Embleton ('08)). Montgomery ('98) even thought that the nucleolar material might return again to the nucleus at the close of the secretory cycle. Prenant ('05) and Benoit ('26) frankly consider nucleolar extrusion to be associated with cellular or nuclear degeneration; and nuclear extrusions have indeed been described as unusually abundant in conditions involving pathological degeneration. Refer, for example, to Adami ('06), and Hanitzsch ('13); and also Heidenhain and Werner ('24). To all these sources of doubt must be added the very large number of cases where nucleolar extrusion has not been described as a normal occurrence in gland-cells, and in certain conspicuous instances has been emphatically denied; as, for example, the conclusion of Yamanouchi ('22) on the lepidopteran silk-gland—a classical source of accounts of nucleolar extrusion (refer to page 318)—and the severe criticism of Montgomery's ('98) account of the gland-cell nucleoli in *Piscicola* by Jörgensen ('13), who was unable to find any trace of nucleolar extrusions. So far as the present literature permits any opinion at all, we must accordingly conclude that even if nucleoli are extruded, their exact connection with glandular activity remains in doubt.

The argument for nuclear participation in secretion thus falls back in the end upon indirect evidence such as Korschelt ('89) so cogently urged. The extraordinary nuclear changes which sometimes occur in invertebrate gland-cells are assuredly difficult to account for on any other basis than one of real relationship of some kind with secretory activity. Nevertheless, the stubborn fact remains that in vertebrate gland-cells variations in position shape, size and staining capacity are not conspicuously exhibited by the nucleus. In many cases the nucleus behaves more as though it had no part in the secretory activities of the cytosome (Bowen, '26d); and Duesberg ('12) concluded that the changes might just as well be explained as evidence of the influence of the cytoplasm on the nucleus, rather than vice versa. M. Heidenhain ('07), indeed, rejected the argument for nuclear coöperation in secretion on the ground that the changes might be equally well interpreted as indicative of "regenerative" operations presumably necessary in cells of such pronounced activity. To my mind, however, the conditions in certain invertebrates can scarcely be so easily dismissed, and it is difficult to avoid the conclusion that these changes really are directly associated with some phase of secretory synthesis.

To conclude, it appears that in general the nucleus has been pretty definitely shown not to be the immediate source of secretions. On the contrary it exhibits much less visible connection with secretory processes than we might have anticipated on a priori grounds. Secretion is a function in which all parts of the cell may very probably be called on for their contribution toward the end-result, and in this process the nucleus seems to do its bit. What this may be in more exact terms, we do not know. Perhaps it is merely a regulative function, or the nucleus may synthesize certain materials required in the cytoplasm for, or as a result of, secretion. Such a conception of nuclear function in secretory activity in terms of some coöperative, as yet intangible, association with the cytoplasm, has indeed been often proposed, recent examples being Lutz ('21), Bowen ('26d), and Tschassownikow ('27). This is admittedly an unsatisfactory and dubious conclusion, but the facts do not warrant anything more definite. Certainly the oft-repeated statements touching on the supposed importance of the nucleus in secretion have a very inadequate and unreliable cytological foundation.

NOTE:—A complete literature list of references from both the first and second sections will be given at the end of the second part.

(*To be concluded*)

THE INFLUENCE OF THE THYROID GLAND AND HYPOPHYSIS UPON GROWTH AND DEVELOPMENT OF AMPHIBIAN LARVAE

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THE amphibians are an unusually favorable group for an investigation of the problem of development from larval to mature form. The transformation from the tadpole to the frog is spectacular, involving rapid deep-seated changes in the entire organism, and there are many criteria by which this process may be measured; as, for instance, the shortening of the intestine, the development of the mouth, the shrinkage and disappearance of the tail, and most significant of all, the development of the limbs. The last named feature gives us the most accurate criterion of all for measuring the degree of development.

The metamorphosis of urodele larvae is not so spectacular, but is none the less significant. B. Zawadowsky ('28) has divided the process of metamorphosis of the axolotl into five stages, during which there is regression of the gills and of the fin folds, protrusion of the eyes, and development of the salamander color pattern. In addition to these criteria, Uhlenhuth has called attention to the fact that the epidermis is shed by urodele larvae often in a single piece at the beginning of metamorphosis, giving the first evidence of that process. He considers the development of the limbs to be of minor significance as indicators of metamorphosis in this group because of their appearance and differentiation in early larval life long before the true evidences of metamorphosis appear as a result of thyroid functioning. This difference in the significance of the limbs as indicators of metamorphosis in the anurans and urodeles is but one of the many points that serve to show that each type, each species, has its own pattern of development; it reacts in its own peculiar fashion to the stimulus that induces metamorphosis.

THE THYROID GLAND

It has long been known that the cretin type of human dwarfism is due to thyroid deficiency, and that this can be remedied by thyroid feeding if administered in time, but it remained for Gudernatsch ('12, '14) to show that the metamorphosis of tadpoles can be enormously hastened by feeding them thyroid material. In his work he used sheep thyroid, but investigations since his time have shown that thyroid glands of any vertebrate can exert this influence when fed.

The most extensive work in the study of the influence of thyroid glands from different types of vertebrates was done by Dr. Horace Gunthorpe at the writer's suggestion. This work is as yet unpublished. It shows that the thyroid glands of all forms of vertebrates studied—fish, whale, sheep, cattle, dog, cat, pig, etc.—can be used to induce metamorphosis, and that each has a specific potency which is not always proportional to its iodine content, as one might assume.

Thyroid feeding is usually soon or later fatal to the tadpole, depending upon the amount administered and the stage of development that the tadpole had previously reached. The larger tadpoles are more readily brought to metamorphosis than those of smaller size. This experiment of inducing amphibian metamorphosis by feeding thyroid material has been repeated innumerable times and is so simple that it can be made a standard experiment in elementary laboratory classes.

Gudernatsch ('12, '14) states that the feeding of thymus glands to tadpoles produces the opposite effect of inhibiting metamorphosis. Swingle, repeating this work with calf thymus, failed to substantiate this phase of Gudernatsch's experiments. Allen ('20) removed the thymus glands of *Rana pipiens* and found that no change in the course of development was produced. Uhlenhuth ('19) showed that feeding thymus material to larvae of *Ambystoma* appeared to retard or prevent metamorphosis only in a few cases when used as the sole food; if mixed with normal food there was no evidence of it—thus leading him to the conclusion that its apparent effect was due to the deficiency of metamorphosis promoting substances in some parts of the thymus substance, not to any retarding influence of that gland.

The action of the thymus gland does not form a part of our subject, and only comes in question here in that it is not found to work in opposition to the thyroid gland, as Gudernatsch claimed.

Effect of removal of thyroid gland

It is desirable in most cases to test out the results of glandular administration, such as feeding or implantation, with experiments in which the gland is removed. Work in this field carried out independently by Allen in 1916 and by E. R. and M. M. Hoskins in the same year, confirmed the results of thyroid feeding in that removal of the thyroid prevents metamorphosis; thus showing clearly that the thyroid gland is normally indispensable to metamorphosis. In these experiments the anlage of the thyroid gland is removed soon after its appearance: at a stage of 5 or 6 mm. total length, in the case of *Rana pipiens*. The operation necessitates the use of a very delicate knife, made from a medium-sized needle by breaking off the eye, inserting the point into a wooden handle, and sharpening to a fine knife edge upon a whetstone. Fig. 1. This must be so well done as to pass muster under a medium power of a binocular microscope. Using an instrument with erect image, the tadpole is laid on its side under water on a paraffin surface and the cut made as shown by dotted line in the diagram. Fig. 2. The removal of the thyroid anlage is then a very simple matter, a little practice making possible the removal of forty per hour. The writer has removed over 250 in one day, with better than 90 per cent success.

In these experiments, the removal of the thyroid gland anlage at its inception gives the clearest possible picture of its rôle in development, because we here have to do with tadpoles in which the gland never has functioned. The absence of the thyroid gland does not affect the rate of growth in size (Allen, '18–'28; Hoskins, '19), nor does it affect the process of early development up to a definite stage that differs in different species. In *Rana pipiens* development ceases at a period shortly after the appearance of the hind limb buds and before they reach a length of 1 mm. Up to this stage in normal tadpoles there is no accumulation of colloid in the thyroid glands in *Rana pipiens*, and as a consequence, these remain small.

In *Ambystoma microstomum* both fore and hind limbs begin to grow before any colloid is formed in the thyroid gland. In *Bufo americanum* it appears almost immediately after the hind limbs have begun to grow, while in *Rana pipiens* it appears practically simultaneously with the anlage of the hind limbs (Allen, '18). In *Bufo americanum* the hind legs continue growing until they soon reach a length of 1.5 mm. at the stage when the operated tadpoles begin to show limb growth different from that of the controls. The leg length in *Bufo* is more significant than at first appears, because the tadpoles of *Bufo* are much smaller than those of *Rana*, and the relative difference in development of the limbs is thus accentuated. The tadpoles of *Bufo* continue to grow, attaining a length of trunk over twice that attained at the stage of development arrest. In these giants the hind limbs may reach a length of 7 or 8 mm. and an increased degree of differentiation. This is in contrast to the condition of *Rana pipiens*, where growth of the hind limbs little exceeds the general proportions to body size at the stage of development arrest and where there is no evidence of continued differentiation (Allen, '25).

It might be argued that during these earlier stages there is such slow secretion that the colloid is used up as rapidly as it is formed. This seems to be disproven by the fact that thyroidectomized tadpoles reach this stage as soon as do the normal tadpoles. It is possible that the slight accumulations of colloid in young tadpoles might not contain the essential substance of the secretion thyroxin at this time. No determinations regarding potency of the earliest colloid of tadpoles have yet been made. Administration of the thyroid glands of young pig embryos shows that they are capable of inducing metamorphosis at the earliest stages at which colloid appears in the follicles (Hogben and Crew, '23).

From this point on, the difference in development between thyroidectomized and normal tadpoles is most striking. The former continue to grow in size and the development of internal organs and external features proceeds in the absence of thyroid secretion to a definite stage, beyond which further development is possible only in response to the stimulus given by the administration of iodine or some of its compounds or by thyroid implantation. In normal tadpoles the thyroid secretion accumulates very rapidly after the gland becomes active and the development toward metamorphosis keeps pace with its increase in size (Allen, '19).

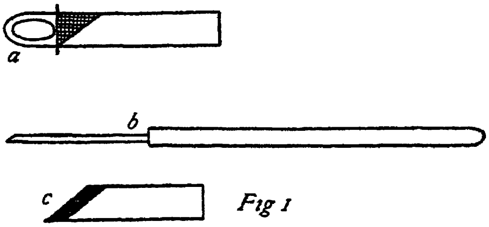

Fig. 1. Method of Making the Knife for Performing Operations upon Tadpoles

a, Breaking off the eye of the needle. *b*, The knife mounted in its handle. *c*, The cutting edge.

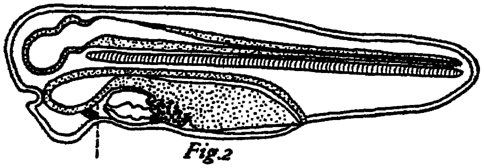

Fig. 2. Diagram of Sagittal Section of Tadpole to Indicate Position of Thyroid Gland Anlage, Shown in Solid Black, and Plane of Cut as Shown by the Dotted Line

The extirpation of the thyroid gland not only inhibits development toward maturity in external features of body form, but equally affects all other somatic characters studied, even the internal organs: as, tongue, intestine, stomach, pancreas, persistence of pronephros, bladder, ossification of the bones (Terry, '18), and brain development (Allen, '18). Hoskins ('19) claimed that the brain continues to develop to an appreciable degree in the absence of the thyroid gland. This was contested by Allen ('24) who claimed, upon the basis of a study of transverse sections, that the apparent growth in the cerebral hemispheres and other parts of the brain is due only to an expansion of the ventricles, and does not involve a true thickening of the brain walls.

Development of gonads independent of thyroid

In contrast to the complete dependence of the development of the somatic structures upon the thyroid gland, is the independence of the gonads. This was demonstrated by Allen ('18), who showed that the gonads continue to develop in thyroidectomized tadpoles of *Rana pipiens* until ripe sperm are formed. This does not occur in normal tadpoles until several months after metamorphosis. It was similarly shown that the ovaries and the contained oocytes develop to a size far beyond that reached at metamorphosis. Hoskins ('19) made substantially the same observations in thyroidectomized *Rana sylvatica*. Swingle ('18) showed the converse of this: namely, that feeding thyroid preparations to tadpoles does not accelerate the development of the germ cells or germ glands. This development of the gonads independently of the soma is in line with the well known case of the axolotl in nature and many other cases of paedogenesis.

In this connection we might well consider the interesting investigations of several workers who have shown that different organs or sets of organs have different thresholds of response to thyroid stimulation, or that there may be organs that are wholly unaffected by it. Uhlenhuth ('21) contends that the limbs of larval salamanders are not under the control of the thyroid gland, and states that when iodothyrine is fed to the larvae of *Ambystoma opacum* at a sufficiently early stage rapid metamorphosis of the body is induced without affecting the limbs; resulting in the production of a salamander with poorly developed hind limbs, which may not have the full number of toes. Conversely he claimed that he was able to inhibit metamorphosis of this salamander by feeding thymus preparation—iodine-deficient food—without, however, affecting the development of the limbs, which grew out of proportion to the body as a whole. Blacher ('28) has done a most interesting and suggestive piece of work along this line. He studied the threshold of stimulation necessary to induce development of different features in the tadpole as measured by different dilutions of thyroidin. The tadpoles were immersed in a given solution for three days; at the end of which time they were killed and measurements taken. He found that the intestine responded to as weak a solution as 0.002 per cent. Twice this concentration was required to stimulate the growth of the tail. Growth of the trunk, the shedding of the horny larval jaws, and the emergence of the fore-limbs required twenty-five times the amount necessary to induce growth of the intestine. When the concentration rises above a given optimum point, stronger concentrations do not produce as great a response as does the optimum strength. Blacher considers the objection that certain processes might respond less quickly and less readily because of their complex character; the emergence of the fore-limbs being an example. He holds that there is a true difference in the threshold of stimulation aside from the differences in the complexity of the parts involved.

Uhlenhuth ('19) attacks the view tentatively advanced by the writer (Allen, '18), regarding the significance of continued development of the gonads of thyroidectomized tadpoles after further differentiation of the somatic structures has been inhibited as indicated above. He states,

> Development of the skin coloration, as well as development of the legs, sex organs, tongue, and palatal teeth are all caused by substances not identical with the substances causing metamorphosis, and since they are all independent of each other in their development, it is probable that special chemical mechanisms exist for the development of each one of these six groups.

A review of this character is not the occasion for a lengthy controversy upon points of difference. The writer would be the last one to contend that development is a rigid process from which there may not be deviations in the case of individual organs. There must be many factors at work, internal and external, and it is quite reasonable to suppose that the different structures may have different thresholds of response to stimuli. Certain structures like the legs of urodeles appear early in development and are not affected by metamorphosis as they are in the anurans. Each species certainly has its own peculiar pattern of response to the stimulus of the thyroid gland. In spite of all this, it does seem to the writer significant that the gonads in both urodeles and anurans develop to a high degree, even to sexual maturity, while the body as a whole remains in its larval condition. This is especially significant in the case of the removal of the thyroid gland—one single factor—which brings about such a sharp distinction between soma and germinal tissue while all the external factors are uniform.

Effect of thyroid on non-metamorphosing amphibians

Reference has already been made to the fact that different types of amphibians react in different degree to the influence of the thyroid gland. It may be well for the sake of our readers who are not zoologists to explain that axolotls, of which mention has been made above, are members of a species of salamander—*Amblystoma tigrinum*—that have retained their larval form and aquatic habit of life far beyond the period when other members of the same species have undergone metamorphosis into land inhabiting salamanders—in other words the axolotl has failed to metamorphose as regards all of its somatic characteristics and yet has become sexually mature. Such cases occur in certain regions such as the plateau of Mexico, and our own Rocky Mountain region of Colorado. The Colorado axolotls transform more readily when removed from their natural habitat than do the Mexican forms.

Necturus, the mud-puppy of the lakes and streams of the Mississippi Valley, is classified as a Perennibranchiate because it retains its gills and full larval character throughout life. It is naturally of interest to study the thyroid glands of these forms and to determine by experiment whether metamorphosis into a salamander form is possible.

In a brief abstract the writer (Allen, '18) showed that the thyroid gland of the Colorado axolotl is of much the same structure and of equal size with that of the normal metamorphosed form of the same species, and that colloid is present to the same degree in both. Swingle ('22) demonstrated that the thyroid glands of the Colorado axolotl are capable of inducing metamorphosis in other forms. He cut up the thyroid glands of a single axolotl, *Amblystoma tigrinum*, into six pieces, and implanted them into immature larvae of *Rana clamata*, causing five of the latter to undergo metamorphosis.

In 1918 the writer carried out unpublished experiments in feeding Armour's powdered thyroid gland substance to adult Necturus, but failed to produce any tendency toward metamorphosis. Swingle ('22) repeated this experiment, likewise without result. It remained for Gutman ('26) to attain a slight measure of success in this line by immersing young Necturus 37 mm. in length in dilute solutions of thyroxin, the essential secretion of the thyroid gland. This alone produced no results, but was effective when used in conjunction with adrenalin. There was advanced reduction of the gills and distinct exopthalmos with change in the form of the head. The larvae invariably died before undergoing any complete metamorphosis. Further work along these lines must prove extremely interesting. Swingle ('22) demonstrated the fact that the thyroid gland of Necturus is capable of producing an active secretion by transplanting ½ the thyroid substance of an adult Necturus into an immature larva of *Rana clamata*, thereby greatly hastening metamorphosis.

Is this failure to metamorphose even when large quantities of the active thyroid secretion have been elaborated and stored up by the animal's own glands due to an inability of the tissues of the animal to respond to the stimulus of the secretion or is it due to the absence of a "releasing mechanism" as claimed by Uhlenhuth ('19)?

Swingle ('24) removed the thyroid glands from Colorado axolotls 7.5 inches long, broke them up, and injected the contents intraperitoneally into the individuals from which they were removed. Two months later there were no evidences of metamorphosis. In a later series, two sets of thyroid glands were injected into each animal; likewise without results. This procedure may not constitute a fair test, because absorption through the peritoneum may not be equivalent to that through the blood stream. Assuming that the procedure affords a fair test, the conclusion would be that we do not have here a failure to respond to a "releasing mechanism" as stated by Uhlenhuth ('19) etc., but a failure on the part of the axolotl to respond to its stored thyroid secretion—sufficient, as shown above, to induce metamorphosis in several tadpoles of other species, as Swingle ('22) demonstrated.

The process of thyroid secretion

While it is not within the scope of this review to enter into an exhaustive discussion of the process of secretion in the thyroid gland, a brief survey will help to a clearer understanding of our problem. The most comprehensive studies of the secretory activities of the thyroid glands of amphibians have been made upon salamanders by Uhlenhuth ('27, '28), who bases his results upon studies both of fixed and of fresh material stained with intra-vital stains. The gelatinous secretion "colloid" is stored in the follicles and discharged from them through the investing layer of secretory cells into the surrounding blood vessels. Uhlenhuth ('27) finds that the secretion is first seen in the cells in the form of small granules that unite into larger droplets. These are of two kinds: chromophobe and chromophile, both of which are discharged into the lumen of the follicle, there to be consolidated into the colloid mass. The chromophile secretion appears as acidophile droplets that accumulate in the apical ends of the secretory cells directed toward the cavity of the follicle. They diffuse into the follicular cavity and after a time change to a basophile condition. The chromophobe secretion is produced in the basal part of the cell, and collects in the intracellular (Anderson) vacuoles, migrates to the apical pole, and passes into the cavity, where it collects to form the "colloid vacuoles" which Uhlenhuth considers to be an essential element of the thyroid secretion. He traces the passage of the secretion through pores between the epithelial cells of the follicles.

According to Uhlenhuth there is a gradual production of thyroid secretion during larval life, becoming more active shortly before metamorphosis and in periods of adult life. These periods of activity are characterized by a decided thickening of the secretory cells, which become columnar in section. They also show increased numbers of secretion granules. The discharge of the secretion results in a sudden decrease in the colloid content of the follicles. After such a discharge there follows renewed activity in colloid secretion. The production of secretion and its discharge into the follicle is continually taking place, and is an elementary function of the thyroid gland. The discharge only occurs in response to external stimuli which are imparted by a special discharge mechanism. In another paper Uhlenhuth ('27) states his view that the anterior lobe of the hypophysis performs the function of a discharge or releasing organ, enabling the thyroid gland to throw its load of secretion into the blood stream. We shall discuss this point in a later portion of this paper.

Huxley ('20) demonstrated the possibility of inducing metamorphosis in the axolotl by feeding it thyroid preparations. We must keep in mind the fact that its own thyroid glands have the potency demonstrated by Swingle and yet do not induce any tendency toward metamorphosis during the years that the axolotl may remain in its larval condition. This, together with the fact that Swingle ('24) failed to induce metamorphosis by injecting the axolotls' own crushed glands even in double dose, would lead us to infer that the axolotl is only able to respond to thyroid secretion superior to its own either in quantity or quality.

Is the thyroid influence exerted directly or through the nervous system?

Some interesting studies have been made upon the question of whether the thyroid influence is exerted directly or through the medium of the nervous system or other surrounding factors. Huxley ('25) kept half-grown larvae of *Rana temporaria* that had been fed with fresh ox thyroid, in solutions of urethane, where they remained thoroughly narcotized for eight or ten days. The process of metamorphosis proceeded at the same rate as in similarly fed tadpoles that were not kept in a state of narcosis. This experiment was varied by keeping them in solutions made from thyroid tablets, but the results were the same. He also performed experiments of a different nature where metabolism was directly affected. Potassium cyanide in weak solution had a retarding effect upon metamorphosis of tadpoles to which thyroid material was fed. Huxley produced the same interference by subjecting the containers in which the tadpoles were kept to an atmosphere of oxygen. This treatment probably does not involve the nervous system at all but acts directly to lower the responsiveness of the tissues. This at least could be easily understood in the case of the potassium cyanide treatment. These results found verification in the later work of Spaul ('28), who extended the experiments to deal with the influence of the hypophysis; which we shall consider later in its proper place. One interesting feature of his work in this connection is his demonstration that the metamorphosis of thyroid-fed tadpoles is retarded by subjecting them to the influence of X-rays.

Returning to the more crucial question of the relation of the developing organs to their surroundings—and the nervous system—we may refer to the work of Helff ('27), who made autoplastic transplantations of the tongue to the back of normal tadpoles. Muscles, glands, and papillae developed in normal fashion in spite of the abnormal position and innervation. The writer can testify that the tongue remains in a rudimentary condition in thyroidectomized tadpoles. We are quite ready to accept Dr. Helff's interpretation that its differentiation is controlled by the thyroid hormones. An interesting addition to this experiment would be the transplantation of the tongue from normal tadpoles to the backs of thyroidectomized individuals.

Iodine as a constituent of the thyroid secretion

It has long been known that iodine is the most essential element in the thyroid secretion. The thyroid gland is the only organ in the body that contains any considerable amount of it. Marine and Rogoff ('16) showed that when iodine is injected into an animal it is fixed by the thyroid gland in a few minutes. Efforts to isolate the essential thyroid secretion have been numerous. Baumann ('95, '96) isolated iodothyrin, which contains the active substance, but not in a pure form. Investigations by Kendall ('14, '17, '19) and later by Harington ('26) showed the pure form of the active secretion of the thyroid gland to be a substance which Kendall named thyroxin. Regarding the exact chemical formula for thyroxin, there is some difference of opinion between Kendall and Harington; the former giving it as $C_{11}H_{10}O_3NI_3$ with one benzine ring, and the latter making it $C_{15}H_{11}O_4NI_4$ with two benzine rings. It is not within the scope of this article to go into questions of biochemistry, but we shall hope to touch upon some of the more significant experiments upon the influence of this and other iodine compounds upon amphibian development. Morse ('14) experimented with various iodine compounds which he applied to tadpoles in an effort to determine the active substance of the thyroid secretion. He immersed tadpoles in solutions of iodine, potassium iodide, iodobenzoic acid, iodoxy-benzoic acid, without producing any tendency toward metamorphosis. Strangely enough, he fed them starch iodide without producing any symptoms of metamorphosis. This is quite similar to the method first successfully applied by Swingle. It is hard to account for Morse's failure, unless he may not have allowed a sufficient length of time. Immersion in solutions of iodine salts is slow in inducing metamorphosis.

Swingle ('18) brought about the metamorphosis of *Rana pipiens* by feeding tadpoles a mixture of iodine and flour. The iodine enters into a very loose association with the starch of the flour, and we get the effect of pure iodine. This was eaten by the tadpoles in quantities vastly greater than met with in normal food and water. Metamorphosis occurred in much the same fashion and in about the same length of time as produced by thyroid feeding. We might assume that the tadpoles had used this rich supply of iodine to synthesize thyroxin by means of their immature thyroid glands, but this explanation was disproven by Swingle's work in feeding the same food to thyroidectomized tadpoles and attaining the same results. At the same time the writer

(Allen, '19) fed the iodine and flour mixture to Rana and Bufo tadpoles that had been hypophysectomized and to those from which both the hypophysis and thyroid gland had been removed. It will be shown later that the presence of both the thyroid gland and the anterior lobe of the hypophysis is essential to metamorphosis under normal conditions of food and water. Yet with relatively large doses of iodine, the tadpole is able to undergo metamorphosis without them. One can only conjecture whether the various tissues of the body are capable of directly using the inorganic iodine or whether certain organs may take over the rôle normally played by these endocrine glands. We thus conclude that so far as metamorphosis is concerned, one of the functions of these two glands is to enable the tadpole to make use of the minute quantities of iodine that occur in the normal environment.

The function of the thyroid glands in this connection is well illustrated by Swingle's ('19) finding that metamorphosis of normal Rana larvae could be induced by a concentration of iodine below 0.0000003833 per cent—the weakest used in his experiments, but double this concentration was insufficient to induce metamorphosis in thyroidectomized tadpoles even when they were exposed to it for fairly long periods of time.

Between iodine and thyroxin is a great gap, and many experiments have been performed upon iodine compounds of intermediate degrees of complexity; but it is not always easy to evaluate these findings because of the various means of administration; such as feeding, peritoneal implantation, injection, and immersion in weak solutions, so the results are far from possessing quantitative value. At the same time, it is well to note that Swingle ('19) found a marked difference in the effects of certain simple inorganic iodine compounds. Iodine alone was most potent, while next in order were iodoform and potassium iodide. Potassium iodate was eaten by the tadpoles, but did not cause metamorphosis in Swingle's experiments. He considers this to be due to an inability of the tadpole to break down the molecule and release the iodine.

Passing to the more complicated substances, Morse ('14) stated (page 426) "It is clear that the iodine-bearing portions of the thyroid substance, that is, thyreoglobulin and iodothyrin, give results which can not be distinguished from those obtained by feeding the desiccated powder or tablets." He also showed at the same time that 3–5 di-iodo-tyrosine induces metamorphosis, but not as readily as intact thyroid substance.

Abderhalden and Schiffmann ('22) verified this last point and likewise showed that di-iodo-tyramine and several other substances of character similar to these likewise induce metamorphosis. They failed to attain this result by feeding iodo-acetyl di-iodo-tyrosine, B-iodo-propionic acid, and tyrosine. Romeis ('22) also induced metamorphosis in tadpoles by the use of di-iodo-tyrosine, but found that it was not as active as thyroxin.

Abelin ('21) made extensive studies on the influence of inorganic and organic iodine compounds; among the latter being tyrosine and di-iodo-tyrosine. His work showed that iodine is the essential constituent of these substances in inducing metamorphosis.

These results with tyrosine and di-iodo-tyrosine were verified by Swingle ('22), who induced metamorphosis in thyroidectomized and hypophysectomized larvae of *R. sylvatica* by feeding di-iodo-tyrosine. He then proceeded to demonstrate in clear fashion the significance of iodine in its association with amino-acids by feeding pure tyrosine to one set of tadpoles, 3–5 di-iodo-tyrosine to a second set, and 3–5 di-brom-tyrosine to a third set. In this series only the combination containing iodine was shown to induce metamorphosis. Bromine, although akin to iodine, was thus shown to have no effect when it was used to replace the iodine, and administered under identical conditions.

Kendall ('19) showed that acetylated thyroxin had lost its power of affecting basal metabolism when applied to mammals, but that it had lost none of its capacity for inducing metamorphosis in amphibians. Swingle, Helff, and Zwemer ('24) repeated and extended this work, fully substantiating the findings of Kendall.

Gayda ('22), feeding and injecting thyroid gland material of warm-blooded animals into such cold-blooded forms as frogs, caused only slight heat production. Oxygen consumption, on the other hand, was shown by Huxley ('25) to be increased 100 per cent in larvae of *Rana temporaria* as a result of exposure to moderately strong thyroid solutions for periods of four to six days.

M. M. Hoskins ('27) has given good evidence to show that acetylated thyroxin accelerates development of new-born rats, when injected hypodermically. It will be of much interest to further extend these experiments upon young mammals to determine whether the element iodine or its simpler compounds can produce modifications of early development comparable to the influence that they exert upon amphibian metamorphosis.

We may well accept the conclusion that this effect is quite different from the metabolic stimulus that can only be exerted by the unmodified thyroxin. There has been, in general, a tendency among investigators to emphasize the differences in the influence of iodine and its compounds upon amphibians and upon mammals. Color is given to such a view by the great differences in the readiness with which the reaction to iodine and its derivatives is shown within the amphibian group itself when we compare its effect in the anurans and the urodeles.

Since Swingle's demonstration ('18) no one has seriously contested the finding that inorganic iodine—even the element iodine—can induce metamorphosis of anuran tadpoles when administered in food, when injected, or when mixed in the water in which they live. There is also universal agreement that metamorphosis of urodele larvae can be induced by thyroid feeding, immersion in, or injection of thyroxin, iodothyrine, etc., but Uhlenhuth ('21) as a result of studies upon *Ambystoma*, claims that inorganic iodine has no effect upon Salamander metamorphosis. This is in line with the thesis maintained by Uhlenhuth to the effect that the process of manufacture and storage of thyroid secretion does not insure its release, which can come only through the agency of a releasing mechanism, with which the administration of inorganic iodine has nothing to do.

On the other hand, Huxley and Hogben ('22) metamorphosed Salamander and Triton larvae by immersion in dilute solutions of iodine. In the case of *Necturus* and other urodeles, it is much more difficult to induce metamorphosis by means of inorganic iodine, and efforts have been made to accomplish this by immersion in solutions and injection of solutions, but they have failed to attain results. Huxley and Hogben ('22) fed iodine to the Axolotl, but failed to cause it to show any signs of metamorphosis. Later Huxley ('25) repeated the feeding experiments and in addition kept axolotls in iodine solutions, but only succeeded in inducing some of the changes associated with the early stages of metamorphosis.

Success in inducing metamorphosis of the axolotl by means of inorganic iodine has been attained by Abelin ('21) Hirschler ('22), Blacher and Belkin ('27) and by Zawadowsky, Raspopowa, Rolitsch, and Umanowa-Zawadowskaja ('28). The last named group of investigators attempted to induce metamorphosis of this form by immersion in iodine and Lugol solutions, and by injection intraperitoneally, but this treatment has given only equivocal results. Hirschler was successful through peritoneal implantation of a crystal of iodine encased in cotton and collodion. This method was modified by Blacher and Belkin, who wrapped the iodine crystal in a thin sheet of cotton moistened with salt solution. B. M. Zawadowsky and his associates successfully repeated this experiment, employing the method of Blacher and Belkin. Ingram ('28) induced metamorphosis in thyroidectomized and hypophysectomized Colorado axolotls by the subcutaneous implantation of iodine crystals.

It is thus clear, so far as the experiments go, that all amphibians which are known to metamorphose under any circumstances can be induced to do so by the proper application of inorganic iodine. In the urodeles, this is far more difficult than in the anurans, and is especially difficult in the neotenous axolotl, where the strongest and most direct application of iodine crystals is necessary.

The administration of organic iodine results in an increase in the amount and density of the colloid secretion in the thyroid follicles. This was shown in amphibians by Swingle ('19) in his work upon *Rana pipiens*. It had been previously demonstrated by Marine and Williams ('08) and by Marine and Lenhart ('09) in man, the dog, and sheep, ox, pig, cat, and fish. The amount of stainable colloid was clearly shown to vary with the amount of iodine available. In fact, these workers have explained the effect of iodine in the treatment of goiter upon the principle that it induces an increase in the amount of colloid stored in the thyroid follicles and that this in turn brings about an involution of the hypertrophied and hyperplastic secretory epithelium.

The effect of goitrous thyroids

While it is far from the purpose of this paper to discuss the goiter problem, we cannot resist the temptation to discuss several papers upon this subject that serve to illustrate the principles of amphibian development. There is indeed a widespread tendency to use tadpoles in biological tests to determine the functional activity of pathological thyroid glands. This type of work is of interest to the biologist not only for the light that it throws upon our problems, but because it tends to demonstrate the practical value of our work.

Among the earlier papers in this field is that of Lenhart ('15), who fed to tadpoles human thyroid glands taken from different types of goiter, simple and exophthalmic types. All produced metamorphosis. Graham ('16) fed tadpoles with material from pathological human thyroid glands and showed that preparations of thyroid gland from adenomatous goiter cases induced metamorphosis but not so readily as does material from normal thyroids. In either case, the influence is exerted by active iodine content. Abderhalden and Schiffmann ('22) performed similar experiments with normal and goiter affected glands, and likewise came to the conclusion that both induced metamorphosis, the speed being directly proportional to the iodine content.

Abelin ('27) fed tadpoles with thyroid

glands affected with various forms of goiter and also administered glands of human and calf embryos. In all of this work he took the iodine content into account and observed a uniform method of feeding the tadpoles. Of the five cattle embryos used, only one had visible colloid in the follicles; four of them, however, contained an appreciable amount of iodine and induced metamorphosis in tadpoles to which they were fed. He concluded that there is no necessary correspondence between colloid content and capacity to induce tadpole metamorphosis, between colloid content and iodine content, nor between iodine content and capacity to induce metamorphosis. He concluded that the active thyroid substance does not first develop as colloid in the follicle cavities, although it is stored there, and that the iodine is not all present in a chemically active combination.

The work of Tatum ('19, '20) developed a clever method of separating the colloid contents from the cellular material of mammalian thyroid glands. He found that iodine occurs both in the cells and in the colloid secretion, mostly, however, in the latter. This determination was made in beef, sheep, and pig thyroid glands. Studies upon the dog failed to demonstrate such quantities of iodine in the cell tissues. Van Dyke ('21) found that there is a constancy in the iodine ratio of the colloid as compared with tissues in the thyroid gland of the dog and man in spite of decided morphological variation.

Cooksey and Rosenblatt ('28) came to very similar results. They likewise found that the effect of pathological thyroid glands upon metamorphosis is not proportional to the iodine content, thus leading us to conclude that much of the iodine stored in the thyroid gland is not in the form of an active substance (thyroxin). They concluded (p. 13):

> Feeding experiments were conducted in which various types of goitrous glands from human beings were fed to tadpole larvae. There is evidence from these experiments that thyroid glands from clinically active cases of goiter actually contain more active thyroid principle per unit weight than the normal thyroid. Other goitrous glands contain less active principle by this biologic test, and the amounts were directly proportional to the clinical activity of the patient. Old non-toxic adenomas contained less active principle per unit weight than normal, while one gland which had had much roentgen-ray treatment and rest also contained less active principle per unit of weight.

These investigations are in line with the unpublished work of Gunthorpe, in which he showed that administration of the normal thyroid glands of different types of vertebrates exerts an influence that is not necessarily proportional to the iodine content.

There is not the slightest doubt that the form in which iodine is combined by the thyroid gland plays a very important rôle in determining its activity. Thus far thyroxin from mammalian thyroid glands has been chemically isolated as the active substance. It is quite possible that other types of vertebrates may form other iodine compounds of similar nature but with potency different from that of thyroxin, and it is possible that there are quantities of iodine held in storage but not formed into thyroxin. It had been fully demonstrated that the functioning of the thyroid gland depends upon the available store of iodine, and we should very naturally suppose that factors influencing the organism as a whole should affect the activity of the thyroid gland in utilizing the iodine that it receives. Adler ('16) made a histological study of the thyroid glands of tadpoles reared under different climatic conditions. Those from the Alps show large thyroid glands with small follicles, while specimens from the coast of the Adriatic have small thyroids containing a few large vesicles, and those taken in middle Germany have thyroids of intermediate character corresponding to the climatic conditions. Tadpoles kept at a high temperature are retarded in their metamorphosis and to a lesser degree in growth, the result being abnormally large size at metamorphosis. If the temperature change be from low to high—10°C. to 30°C.—growth is retarded more than the process of metamorphosis, resulting in a smaller size at metamorphosis. On the other hand, a change from high to low temperature results in a larger size at metamorphosis. Terini ('19) found that a temperature of 28°C. applied to thyroid fed tadpoles caused great acceleration in their metamorphosis as compared with thyroid fed tadpoles at a temperature of 9°-15°C. He pointed out the well established fact that high temperature alone does not cause asymmetrical development, although the administration of thyroid material as food does.

Do the tissues store thyroxin?

Some attention has been given by various authors to the question of continuance of metamorphosis after discontinuance of an initial stimulus. Most observations along this line have been incidental to other lines of investigation and have concerned the discontinuance of thyroid feeding. Investigations of this kind should be tested by careful investigation of the contents of the alimentary tract. A very clever experiment was performed by M. M. Hoskins ('22) in which she removed the thyroid gland of the tadpole and implanted it into the tail. When the tadpoles thus treated had reached maximum size and had well developed legs, she cut off the tail with the implanted gland. In most cases the tadpole completed metamorphosis in response to the initial stimulus.

Abderhalden and Wertheimer ('28) have made an interesting investigation of the capacity of the different tissues to absorb thyroxin from a solution in which they are placed. This problem was attacked in two ways: (1) by feeding to tadpoles various tissues such as liver, muscle, blood corpuscles, etc., that had been soaked in thyroxin solutions; (2) by the reciprocal method of observing the amount of thyroxin removed as determined by placing tadpoles in the solutions into which the tissues had been immersed. In all cases it was shown that muscle tissue has the greatest affinity of all for thyroxin. The muscle absorbs the thyroxin within half an hour, longer immersion causing no further absorption. The thyroxin cannot be boiled, soaked or compressed out of the tissues.

Kahn ('24) fed tadpoles with the tissues of tadpoles that had been stimulated to metamorphosis through thyroid feeding. Such tissues did not induce metamorphosis, showing that they had not stored any considerable part of the thyroid substance fed.

Zavadovsky and Novikov ('26) studied the rôle of the different components of the blood in transporting thyroxin, their results being in line with the later observations of Abderhalden and Wertheimer ('28) mentioned above as regards the erythrocytes. After these had been soaked in thyroxin and later washed, they were incapable of inducing metamorphosis of axolotls into which they were injected. The serum, on the other hand, plays a dominant rôle in carrying thyroxin.

It does not come within the scope of this paper to discuss the influence of the thyroid gland or its derivatives upon invertebrate forms. In general, we may say that the evidence from many investigations upon a great variety of invertebrates themselves possessing no thyroid gland shows that they are not capable of responding to its influence by changes in the nature of metamorphosis or hastened development. Evidence of this among vertebrates outside of the amphibians is scanty indeed, but this is an important field of investigation where a proper comparison can be established between metamorphosis and differentiation.

Ukita ('19) studied the effects of thyroidectomy of pregnant rabbits upon the growth and development of the foetus. He showed that there is great prolongation of the period of gestation and that the young at birth are weak and show incomplete ossification. Their thyroid glands have undergone hypertrophy, and abnormalities are produced in the post natal growth of the bones. These deficiencies are in line with the findings in many cases of cretinism.

The metamorphosis of tadpoles and the process of development in mammals certainly must be essentially comparable, but mammalian differentiation is by no means so spectacular as metamorphosis. We have every reason to hope that experiments upon the influence of the thyroid gland in mammalian embryonic development may prove to be of great theoretical and practical importance; but up to the present time very little indeed has been done in this field.

THE ANTERIOR LOBE OF THE HYPOPHYSIS

In the hypophysis or pituitary gland we have to do with a complex of four different glands that are functionally distinct from one another so far as our knowledge justifies an opinion. The illustration, Fig. 4, indicates these parts and shows their relation to one another. We shall not attempt to discuss the use of the terms hypophysis and pituitary, but shall distinguish them as pars anterior, pars intermedia, pars tuberalis and pars nervosa of the hypophysis. The older accounts distinguished only two portions: the anterior lobe, which corresponds to that part as at present recognized, and the posterior lobe, which corresponds to the pars intermedia and pars nervosa. The pars tuberalis was the last discovered, and has only recently been taken into account. We know very little, if anything, of its function, although it should be possible though difficult to carry out experiments along this line. It is no doubt known to most of our readers that this complex of glands lies under the very center of the brain, occupying in the mammals a deep socket called the sella turcica that constitutes an important landmark in the center of the floor of the brain case.

For many years the hypophysis was known only because it occupies this landmark, not because of any functional significance that was ascribed to it; but the endocrine investigations of recent years have shown it to exert a profound influence upon the body.

Embryonic development of the hypophysis

Before we lose sight of the different divisions of this gland complex, we must take account of the embryonic development. Pars anterior, pars intermedia, and pars tuberalis all develop out of the same anlage growing inward from the surface ectoderm. In the mammals this ingrowth arises from the roof of the mouth and is termed Rathke's pocket, while in the amphibians that concern us here, it arises as a solid tongue of cells growing horizontally inward from the surface ectoderm above the anlage of the mouth. It extends to the infundibulum. After a time it breaks away from the surface ectoderm and differentiates into the anterior, intermediate and pars tuberalis portions of the hypophysis. The pars nervosa, on the contrary, arises from the tip of the infundibulum.

Effect of removal of hypophysis

One of the first methods of attacking an endocrine problem is to study the effects produced by a removal of the gland in question. The earliest work of hypophysectomy performed upon tadpoles was that of Adler ('14). His method was to burn out the gland by applying an electric cautery to the roof of the mouth of the 20 mm. Rana tadpoles. This operation resulted in a very high degree of mortality, and he was able to rear only three specimens out of many hundreds operated. As a result of this operation metamorphosis was prevented—the hind limbs persisting as mere buds many months after the control tadpoles had metamorphosed. Adler also noted that the absence of the hypophysis exerted a profound influence upon the thyroid gland, which was markedly retarded in growth and contained only a small amount of colloid of fluid consistency.

A different method was simultaneously devised by Allen and by Smith in 1916. E. R. Hoskins, B. M. Allen, and P. E. Smith independently contrived a method of removing the anlagen of endocrine glands by cutting them out at their first appearance. Hoskins in New York City operated upon the thyroid gland, Smith in Berkeley, California, removed the hypophysis, and Allen, in Lawrence, Kansas, removed both; each without any knowledge of the work done by the others. Smith and Allen made reports upon their work at the San Diego meeting of the Western Society of Naturalists, August 9–12, 1916. The printed report of Smith's work appeared in *Science*, August 25, '16, and Allen's account appeared in *Science*, November 24, '16. While our method of attacking these problems has been the same, our interests have been along somewhat diverse lines, but where they have converged, we have usually found ourselves in substantial agreement.

This method of removing the buccal anlage of the hypophysis entails little mortality, and has the added advantage of depriving the animal of the gland anlage without leaving a trace and of assuring that we are dealing with animals in which the gland never has functioned to the slightest degree. The operation is performed as shown in figure 3 at the period when the tail bud is first appearing—3.5 mm. to 4 mm. total length in *Rana pipiens*. The wound heals in a short time, and the tadpoles show no serious defects save for an occasional specimen in which the mouth is defective. These specimens can readily be detected and eliminated. The results that we shall discuss are shown to be due to the absence of the glands, and not to the trauma of the operation, as seen by comparison with normal control specimens that had been cut in the same manner and the gland anlage left untouched.

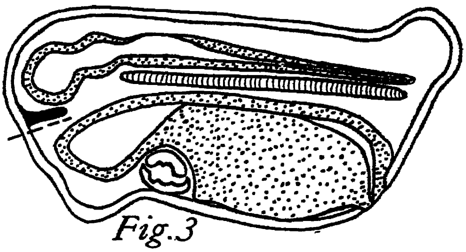

FIG. 3. DIAGRAM OF SAGITTAL SECTION OF TADPOLE TO INDICATE POSITION OF BUCCAL ANLAGE OF THE HYPOPHYSIS, SHOWN IN SOLID BLACK, AND PLANE OF CUT AS SHOWN BY THE DOTTED LINE

It will be recalled that the buccal anlage thus removed is the source from which the pars anterior, pars intermedia, and pars tuberalis develop (figs. 4 and 5). When we use the word "hypophysectomy" we have reference only to the buccal

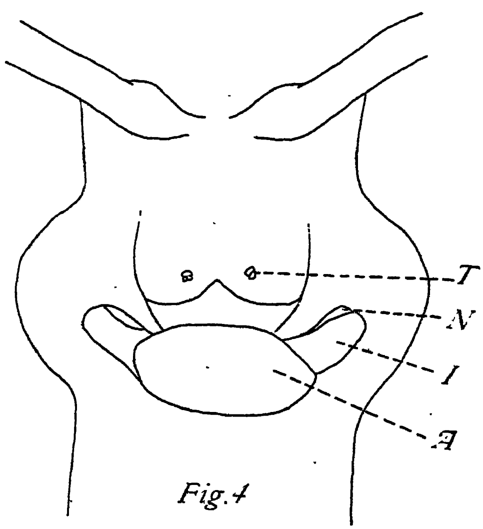

FIG. 4. UNDER SURFACE OF THE BRAIN OF THE ADULT RANA AURORA DRAYTONI SHOWING THE FOUR PORTIONS OF THE HYPOPHYSIS IN SITU

A-Pars anterior; *I*-Pars Intermedia; *N*-Pars Nervosa; *T*-Pars Tuberalis.

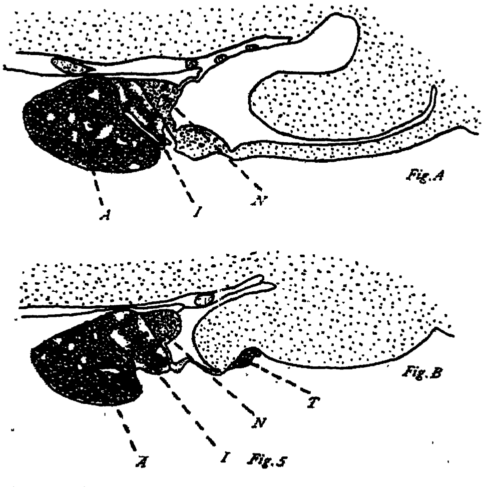

FIG. 5. FIG. 5*a* REPRESENTS A MEDIAN SAGITTAL SECTION OF THE HYPOPHYSIS OF RANA AURORA DRAYTONI. *A*-PARS ANTERIOR; *I*-PARS INTERMEDIA; *N*-PARS NERVOSA. FIG. 5*b* REPRESENTS A PARASAGITTAL SECTION OF THE SAME. LETTERS *A*, *I*, AND *N* AS INDICATED ABOVE. *T*-PARS TUBERALIS

anlage and these three lobes that develop from it. The anlage of the pars nervosa is not touched in this experiment, and it undergoes definite growth in spite of the absence of the other lobes of the hypophysis, as shown by Allen ('17) and by Smith ('20). Smith made a careful quantitative study of the later development of this structure, and showed that it is much retarded in growth and abnormal in form as compared with its condition in normal tadpoles of similar size. In cases of partially successful operations, Smith found that any part of the pars nervosa in touch with fragments of the buccal anlage undergoes hypertrophy, thus appearing to respond to the local stimulus exerted by its derivatives. This is made especially clear in cases where the buccal anlage has suffered some displacement. No physiological evidence has been offered to show whether this "vestigial" pars nervosa has any functional value.

Let us now sum up the complex of effects produced by the removal of the buccal anlage and the consequent total absence of the pars anterior, pars intermedia and pars tuberalis.

They are as follows:

1. Failure to metamorphose.
2. Retardation of growth in size.
3. A striking modification of the pigment cells resulting in the assumption of a creamy silver color in *Rana pipiens* and a less conspicuous color change in other forms.
4. An apparent increase in susceptibility to disease and other unfavorable conditions. This needs statistical treatment, but is obvious to those who have worked along these lines.

It will be our object in this paper to discuss only the first two factors, because they involve problems of development (differentiation) and size growth. It has been definitely shown that the pars anterior of the hypophysis is concerned with both these processes, and we have equally good evidence that neither the pars intermedia nor the pars nervosa is concerned with them. The pars tuberalis is an enigma because of our total lack of knowledge regarding its functions.

Relation of hypophysis and thyroid gland

The interrelations between the thyroid gland and the pars anterior of the hypophysis are quite interesting. Rogers ('18), Larson ('19), Hoskins and Hoskins ('19), and Smith ('20) have all shown that thyroidectomy causes the latter to increase in size, while, on the other hand, Adler ('14), Allen ('16, '17), Smith ('16, '20), and Hoskins and Hoskins ('19) have demonstrated that the removal of the hypophysis causes a retardation in the growth of the thyroid gland and prevents it from storing up colloid secretion. Smith ('20) showed that the thyroid gland of hypophysectomized tadpoles is reduced to one-sixth the normal weight in tadpoles 36 mm. or more in length.

Not only is there practically no visible accumulation of thyroid secretion, but the absence of the hypophysis has the same effect in relation to metamorphosis as does the absence of the thyroid gland. There is no doubt upon this point in the minds of those who have investigated it. Allen ('25) showed that there was the same degree of growth of the hind-legs in tadpoles from which the thyroid gland had been removed, in those that had been hypophysectomized, and in those from which both had been removed. In all three cases of the total absence of both, or the absence of either, the hind limbs develop to the same degree, which is specific to the species in question.

Whatever be the nature of the rôle played by the hypophysis, the secretion formed as a result of its coöperation with the thyroid gland is stored up in the thyroid follicles, not in the hypophysis. Feeding thyroid preparations to tadpoles induces metamorphosis even though the thyroid gland and the hypophysis be absent. We have already called attention to the fact that Allen ('19) caused metamorphosis by feeding iodine to tadpoles from which the hypophysis had been removed and even in those from which both the hypophysis and thyroid glands had been removed.

The hypophysis alone, even when present in unusual degree, is incapable of inducing metamorphosis, or even a tendency in that direction in the absence of the thyroid gland. Allen ('20, '21) demonstrated this point by implanting the hypophysis of adult frogs into thyroidectomized tadpoles. Even in these cases, where the material of the hypophysis was present in excessive amount, there was not the slightest evidence of any progress toward metamorphosis beyond that regularly reached in the thyroidectomized tadpoles, even after a period of many months. The implanted glands maintained themselves during this entire time as shown by a histological study of them made at the conclusion of the experiment.

We stated above that the pars anterior of the hypophysis is the portion of that gland complex that is concerned in coöperating with the thyroid gland to induce metamorphosis. Allen ('21, '27) made implants of the pars anterior, the pars intermedia, and the pars nervosa into hypophysectomized tadpoles; but the pars anterior was alone effective in inducing metamorphosis (fig. 6). We have pointed out that no studies have been made regarding the significance of the pars tuberalis.

It was shown in these experiments that implantations of the pars anterior bring about the secretion of colloid within the thyroid gland, which results in metamorphosis. Histological studies of the thyroid gland during the progress toward metamorphosis showed a progressive accumulation of colloid substance. While there can be no question about the dependence of the thyroid gland upon the pars anterior of the hypophysis, we are still in the dark as to the nature of this relationship.

Smith and Smith ('23) showed that this same result could be produced by repeated intra-peritoneal injections of extracts of the fresh pars anterior of the beef hypophysis, obtained by grinding the sterile glandular substance in sand, diluting with saline solution and centrifuging. Injection of this preparation three times per week restored the thyroid gland of hypophysectomized tadpoles to completely normal function and resulted in metamorphosis of the tadpoles so treated. It is important to keep in mind the fact that metamorphosis was a result of the restoration of the thyroid gland to normal functional activity. This experiment would appear to demonstrate the presence of a secretion in the pars anterior of the hypophysis that influences the thyroid gland or that may contribute substances essential to the elaboration of its secretion.

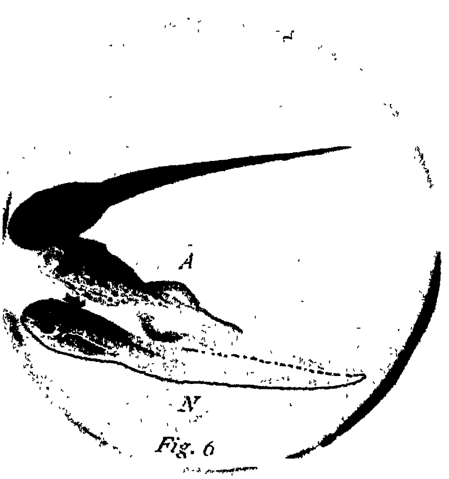

Fig. 6. Photograph of Three Hypophysectomized Tadpoles of Rana aurora draytoni into Each of Which a Different Portion of the Hypophysis of the Adult Frog has been Transplanted

These are as follows: into *A*-Pars Anterior; into *I*-Pars Intermedia; into *N*-Pars Nervosa. The reëstablished development of the Pars Anterior transplant and the color change of the Pars Intermedia transplant are obvious.

Spaul ('25, '28) devised a method of making an extract of the pars anterior of the hypophysis by grinding it up in a 0.125 per cent aqueous solution of acetic acid. When injected at frequent intervals—three times per week—this induced metamorphosis of normal tadpoles. Comparisons of the effects of thyroid and pars anterior injections in uniform weak dilutions showed the former to be far more potent than the latter.

Immersion of tadpoles in pars anterior solutions wholly failed to induce metamorphosis, showing that absorption through the skin and probably also through the alimentary tract fails to induce metamorphosis.

Spaul makes an interesting observation upon the behavior of tadpoles injected with pars anterior extract as compared with those injected with thyroid extract. The specimens injected with the latter made quick rapid movements in contrast with the more quiet behavior of those injected with the pars anterior extract.

Effect of metabolic depressants

Huxley ('25) had shown that KCN or alcohol inhibits metamorphosis through a depressant effect upon metabolic processes when used in sufficiently high non-toxic amounts in the medium. In this way it can to a large degree counteract the influence of the thyroid gland. Spaul ('28) applied the same methods of investigation to determine whether the effects of intra-peritoneal injections of the pars anterior of the hypophysis could be similarly nullified. He found that this was true in correspondence with the findings of Huxley. A similar decrease in the ability of the tissues to respond to the stimulus of the secretions of the thyroid gland or of the pars anterior of the hypophysis was shown in the case of tadpoles that had been subjected to the action of X-rays. These experiments showed the degree to which injury or inhibition of the tissues could lessen their capacity to respond to stimulus.

The nervous system is not involved in the response to these stimuli, as Huxley ('25) showed by narcotizing with urethane. This treatment does not inhibit or retard metamorphosis of tadpoles in response to thyroid extracts in the aquarium medium; thus demonstrating that the hormone does not act through the nerve centers. Spaul ('28) applies the same method of investigation to the treatment with extracts of the pars anterior of the hypophysis and comes to the same results, confirming Huxley's conclusions in this regard.

Unreliability of commercial preparations of endocrine substances

Hoskins and Hoskins ('20) caused normal and thyroidectomized tadpoles to metamorphose by administering to them a commercial preparation of the pars anterior of the beef hypophysis prepared by one of the leading manufacturers of endocrine preparations. They had an analysis made which showed that this preparation contained iodine in the ratio of 1:200,000 in the fresh gland. They did not know the form in which it occurred but assumed that it would be soluble and diffuse into the water of the aquarium in which the tadpoles were kept. They concluded from these experiments that feeding the pars anterior of the hypophysis causes metamorphosis.

Smith and Cheney ('21) repeated this work and likewise produced metamorphosis by feeding tadpoles with the same commercial preparation of anterior pituitary used by Hoskins and Hoskins. They made a crucial test, however, by preparing their own anterior pituitary material from fresh glands and under laboratory conditions. Feeding this material to tadpoles, they did not produce any tendency toward metamorphosis. Analysis showed that the commercial preparation which induced metamorphosis contained 120 times the amount of iodine found in their own laboratory prepared material. Smith and Cheney thus rightly conclude that the pars anterior of the hypophysis does not induce metamorphosis when fed to tadpoles. The whole question is one of contamination of a pharmaceutical product and serves to point a moral regarding the caution that must be observed in the use of commercial preparations in scientific experiments.

This work is completely in accord with unpublished investigations of the writer, who in 1918 induced metamorphosis in *Rana pipiens* by feeding it the same make of anterior pituitary preparation used by Hoskins and Hoskins. When we later repeated the experiment with preparations made in the laboratory from fresh glands, there was no trace of metamorphosis. These experiments were carried out upon hypophysectomized, thyroidectomized and normal tadpoles.

Effect of the hypophysis on metamorphosis in the axolotl

Much interest has been shown recently in the relation of the pars anterior to metamorphosis in the axolotl and the results are rather perplexing. Smith ('22, '23, '26) made intraperitoneal injections of fresh anterior hypophysis extract of cattle into the Colorado axolotl and produced a *retardation* of metamorphosis. Here we have an effect quite the reverse of that produced by Smith ('23) when he applied the same method of treatment to Rana tadpoles both normal and hypophysectomized as described above. This experiment was controlled by injections of Ringer's solution posterior lobe extract and by muscle extracts. Some of his animals were injected with the anterior hypophysis extract alone, while others received a mixture of anterior hypophysis and thyroid gland, serving as an important test for comparing the results with those in which thyroid extract alone is injected. Smith carried out this work in the thorough and careful manner that characterizes his work, with the uniform result of retardation of metamorphosis of the Colorado axolotl.

Hogben ('23) made intraperitoneal injections of a commercial preparation of anterior hypophysis into the Mexican axolotl and caused metamorphosis. Spaul ('24) repeated the experiment, using the same commercial preparation employed by Hogben, and likewise induced metamorphosis. Spaul ('24) in a later investigation tested twelve commercial preparations of pars anterior of the hypophysis and produced metamorphosis with only two of them. Hogben ('27) in his admirable little book upon the internal secretions concedes "Experiments with commercial extracts are however, to be regarded as having doubtful value." This pitfall has been avoided in more recent experiments by Spaul ('25), by which he produced metamorphosis in the axolotl by injecting aqueous acetic acid extracts which he himself had prepared, and Hogben states in his book ('27) that he has attained the same results in unpublished researches. Spaul ('25) attributes Smith's failure to induce metamorphosis in the axolotl to the use of a weaker solution and to contamination with the posterior lobe but this latter objection is hardly a valid one because Smith used a posterior lobe extract as a control and failed to cause retardation of metamorphosis.

Uhlenhuth and Schwartzbachen ('28), by the use of extracts prepared by the method of Spaul, accelerated the metamorphosis of larvae of the Utah axolotl by 36 days as compared with the controls. He adopts Spaul's explanation that Smith's failure to induce metamorphosis is due to contamination of the extract with adherent material of the posterior lobe of the hypophysis. Whether this is the true explanation should be determined by more direct experiments with the posterior lobe itself. The reader will have to judge regarding the merits of this controversy, because the writer feels unequal to the task; although it must be said that the preponderance of evidence is at the present time in favor of the view that the intra-peritoneal extracts of the hypophysis do induce metamorphosis in the axolotl. This would certainly be in line with its universally admitted tendency in anuran tadpoles.

Uhlenhuth and Schwartzbacher ('28) show that intraperitoneal injections of pars anterior of the hypophysis are entirely impotent in inducing metamorphosis of *Ambystoma tigrinum* if the thyroid gland is absent. This was true in larvae of the Utah axolotl form of this species.

In summing up our conclusions upon this point, we may say that *implantation* of the living pars anterior of the hypophysis or frequently repeated intraperitoneal injections of emulsions or extracts of this gland fresh or dried, induce metamorphosis in amphibians provided the thyroid gland is functional. Some may wish to follow Smith in making a reservation regarding the potency of this gland in the case of the axolotl. Even so, that would constitute a special case that would not invalidate the general principle which is now well established. It is now generally conceded that *feeding* anterior hypophysis to amphibian larvae does not induce metamorphosis or any tendency toward it. We can only conjecture as to why this mode of administration is ineffective in accelerating metamorphosis even when the thyroid gland is present. Experimental studies alone can give the answer.

It is furthermore established that the pars anterior of the hypophysis acts upon the process of metamorphosis only through its influence upon the thyroid gland. As to the nature of this influence we again can only conjecture. One point of great significance is the fact that there is no accumulation of thyroid secretion without the influence of the pars anterior of the hypophysis, as is clearly seen in the lack of colloid in the thyroid gland of hypophysectomized tadpoles and its appearance after transplantation of the pars anterior or repeated injection of its extracts. While pars anterior may play an important part as a releasing mechanism for causing the thyroid gland to discharge its secretion into the blood, as urged by Uhlenhuth, the foregoing facts show that it is certainly essential to *production* of the secretion.

Ingram ('28) gives us an insight into the significance of the influence exerted by the pars anterior upon the thyroid gland by showing that heteroplastic transplantation of the pars anterior of the early metamorphosing *Rana clamata* into the slow metamorphosing tadpoles of *Rana catesbiana* accelerates metamorphosis in the latter form. It must be said that he used three gland implants from metamorphosing tadpoles in this experiment and one might be inclined to interpret the accelerated development as a result of the quantity instead of the quality of implanted glandular tissue. Examination of the thyroid glands of the *Rana catesbiana* hosts showed that their thyroid glands had increased to twice the size of those of the controls. The cells of the thyroid glands had increased in length and there was a decrease of colloid secretion. This condition resembles that described by Uhlenhuth as characteristic of the thyroid gland in process of actively discharging its secretion. This experiment suggests the view that the early metamorphosis in *Rana clamata* and the delayed metamorphosis in *Rana catesbiana* might be determined primarily by the activity of the pars anterior of the hypophysis, rather than by differences in the thyroid glands. Much work is necessary to give us the basis of a decision upon this interesting question.

Effect of the hypophysis on growth in size

While it is clear that the pars anterior of the hypophysis affects metamorphosis by enabling the thyroid gland to produce its secretion, it is equally certain that a secretion elaborated by it causes growth in size. Smith ('18, '20) has accurately demonstrated the fact that feeding preparations of the pars anterior induces growth in size and no one has contested this point. The observations of the writer fully bear out his findings in this regard. Smith and Smith ('23) showed that frequent intra-peritoneal injection of pars anterior extracts caused hypophysectomized tadpoles of *Rana boyeli* to increase in three months to a volume three times that of normal uninjected controls, while this treatment caused normal tadpoles to increase in a similar period of time to twice the volume of the uninjected tadpoles. Thyroidectomized tadpoles were even made to exceed their thyroidectomized controls by four times their volume as a result of pars anterior injections.

Not only has growth acceleration been attained by administering anterior hypophysis to tadpoles, but it has likewise been demonstrated by Uhlenhuth ('21, '23) in *Ambystoma*, by experiments in which he fed chopped worms, beef liver, and pars anterior of the hypophysis to different sets of young *Ambystoma tigrinum*. The liver produced an initial acceleration of growth comparable to that caused by pars anterior feeding, but the latter caused persistence of growth long after it ceased in those fed with worms or liver. There thus appeared to be a specific influence exerted by the pars anterior in prolonging the growth period.

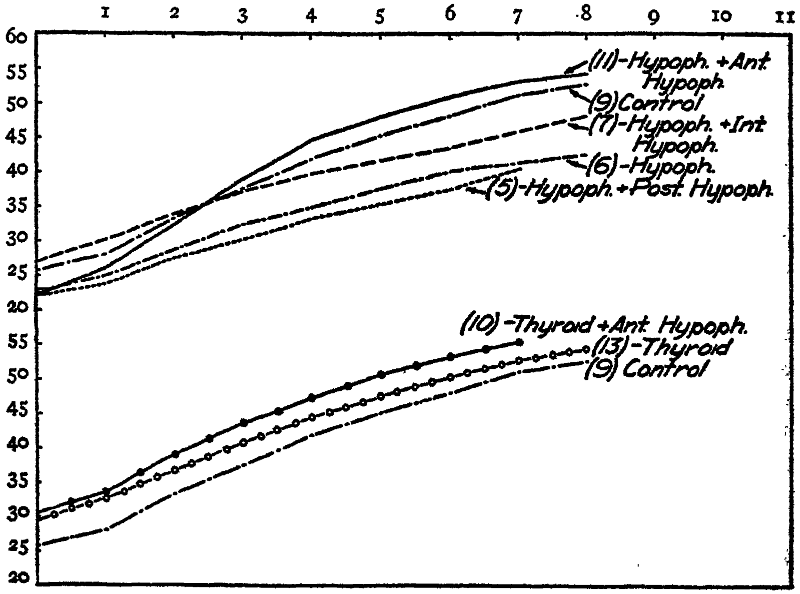

Fig. 7. Graphs Showing the Rate of Growth of Tadpoles of Rana aurora draytoni Studied in 1925

The numbers in parentheses indicate the number of specimens averaged in the group indicated. The abbreviations are self-evident. Controls are normal tadpoles and the line indicating their growth is repeated in the upper and lower group. Ordinates indicate total body length in millimeters and abscissae mark the time from the beginning of the experiment measured in weeks.

Flower and Evans ('25) demonstrated the influence of the pars anterior of the hypophysis in cases of cretinism by choosing sets of three litter-mate young female rats, performing thyroidectomy upon two and then treating one of the latter with daily intraperitoneal injections of pars anterior extracts. The animals thus treated showed normal growth while the thyroidectomized individuals that were not so treated showed all the growth deficiencies of typical cretinism. They concluded that the growth deficiencies of cretinism are due to a disfunction of the hypophysis resulting from the absence of the thyroid gland. This conclusion seems reasonable in the case of the mammals upon which these experiments were performed. In the tadpoles, on the other hand, thyroidectomized individuals keep pace in their growth with normal specimens until the latter begin to undergo metamorphosis. It is difficult to say how large thyroidectomized tadpoles may ultimately grow but they reach twice the total length attained by normal tadpoles during normal larval growth. We are here dealing with continued larval growth rather than accelerated growth. Interesting problems are presented in this field.

Allen ('20, '21, '28) showed that transplantation of the pars anterior into hypophysectomized tadpoles causes them quickly to attain the normal growth in total length that had been denied them by the extirpation of the hypophysis. This treatment likewise appeared to cause thyroidectomized tadpoles to increase slightly in length, and a small number of specimens from which both the thyroid and hypophysis had been removed were made to show growth acceleration in response to implantation of the pars anterior, but the number of cases was too small to give positive proof on this point.

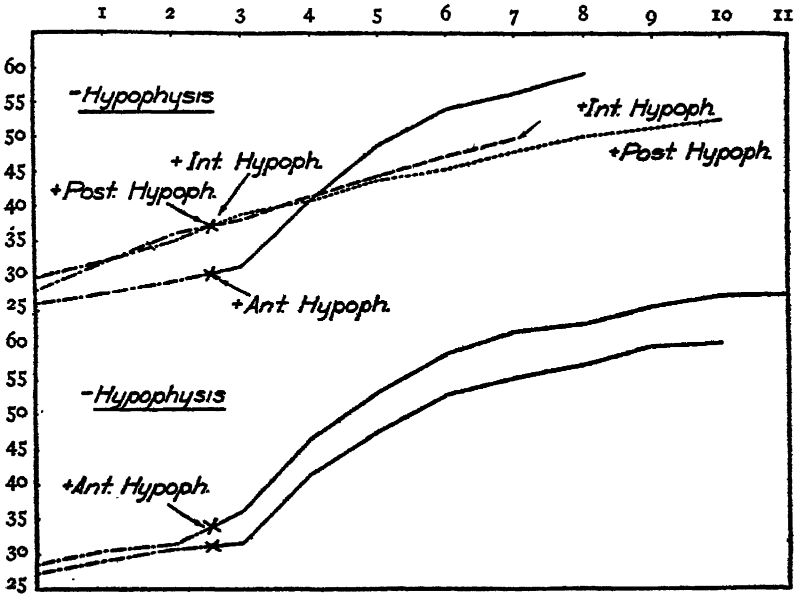

Fig. 8. Graphs Showing Growth of Hypophysectomized Tadpoles of Rana aurora draytoni

At the time marked by X, implants of different lobes of the hypophysis were made as indicated by the abbreviations. The glandular material implanted was in each case taken from the same adult frog. Ordinates indicate total body length in millimeters and abscissae mark the time from the beginning of the experiment measured in weeks.

It is perfectly certain from these experiments that implantation of the pars anterior fully restores growth from subnormal to normal size and that implantation of the pars intermedia or of the pars nervosa has no effect upon growth—neither accelerating nor retarding it. Figures 7 and 8, taken from a recent paper by the writer, illustrate this point. These results are apparently less striking than those of the Smiths ('23), but it must be kept in mind that these are linear determinations as compared with their three dimensional volumes. These experiments should be still further extended to determine the interrelation between the pars anterior and the thyroid gland, but we may safely conclude, especially in view of the striking growths induced by the Smiths in thyroidectomized tadpoles, that the pars anterior of the hypophysis can induce size growth in the total absence of the thyroid gland.

This is most significant in view of the fact that it cannot induce *metamorphosis* without the coöperation of the thyroid gland, which indeed seems to play the chief rôle in that regard. There is much significance too in the fact that feeding the pars anterior induces size growth but does not induce metamorphosis. The fact that there are three types of cells in the pars anterior of the hypophysis—namely, eosinophile, basophile and neutrophile—fits in with these facts to suggest that it produces at least two different secretions, one concerned with growth and the other involved in the functioning of the thyroid gland. That this view is not altogether hypothetical is shown by the fact that Smith ('23) has demonstrated the cortical region of the beef hypophysis to be rich in eosinophile cells, and at the same time especially potent in inducing size growth when fed to hypophysectomized tadpoles; while the central portions in which the basophile cells preponderate show greater capacity for inducing metamorphosis.

It is thus seen that there are many definite conclusions that can now safely be drawn regarding the functions of the thyroid gland and pars anterior of the hypophysis in connection with their control of growth and development. It is hoped that this survey may do more than outline our present knowledge of this complicated field; it will prove far more worth while if it should induce any of the readers to attack some of the many problems that are as yet unsolved. We wish to point out the advantage of using amphibian material. The removal of these glands at their inception, the ease of transplantation technique, the use of injections and of hormone containing media all have served to give us a wonderfully clear picture of the rôles played by these glands, and the field is a large one. Investigations along these lines have just begun.

SUMMARY

1. The thyroid gland and pars anterior of the hypophysis are essential to the continuance of the process of development beyond a definite point characteristic of the species. Absence of either or of both will have the same effect. There is a complete dependence of the development of the organism in all its parts (save possibly the gonads) upon the interaction of these two glands. The secretion thus formed is stored in the thyroid gland.

2. The pars anterior of the hypophysis regulates growth in size, its influence, exerted by various methods of administration, being expressed by a rapid acceleration of growth and probably also by causing its continuance beyond the period when it normally ceases. This stimulus is certainly sufficient to restore growth to normal when administered to individuals in which the pars anterior secretion has been sub-normal or absent, and it appears possible to stimulate growth to a fair degree beyond normal by administration of the pars anterior secretion in various appropriate ways.

3. This function of the pars anterior of the hypophysis whereby it induces growth in size appears to be quite independent of the thyroid gland.

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THYROID AND GROWTH

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THE anatomist sees in the thyroid a bi-lobar structure embracing the trachea (61), the histologist a collection of vesicles containing a pink-staining homogeneous mass surrounded by cuboidal cells (5). The physiologist sees a gland of internal secretion (48), while to the chemist the thyroid is the beaker in which a benzene ring is iodized (36). To the owner of an overly active organ it is an unmitigated nuisance.

These concepts as entities have occupied the time of hundreds of workers who have deluged the scientific and pseudoscientific journals with thousands of articles. It is neither possible nor necessary that a reference list of all this work be made a part of the discussion. The reader who wishes to wander through the capillary bed of the literature will find the chief points of departure indicated in the references which are given, and in the compilations of Biedl (3), Swale Vincent (81), and Sharpey-Schafer (73).

The statement that the chief function of the thyroid is a regulation of the metabolic rate (38), while true, epitomises the point of view of the laboratory worker, in that it envisages no relation of this fact to the broader biological aspects of the phenomenon. The biologist, given the limited conclusion, wishes to know what factors are of influence in changing the functional capacity of the organ, what the results of these changes are in the individual, and what they imply as to the part played by the structure in organic and human development, or growth in its widest sense.

The phenomenon of growth is ubiquitous and of importance to man. From the growth and productivity of vegetable life (44), to the growth of man as an individual (69), and in the mass as populations (58), not to omit the aberrations such as cancer which destroy life (16), the question of growth is inextricably tied up with all matters of human interest. It is from such a point of view that this presentation of the relation between thyroid and growth is made.

The environmental factors known to influence the level of thyroid activity will be first considered. It is convenient to group them into endogenous and exogenous. It is not to be understood that this division implies a lack of inter-relationship, for quite the contrary is the fact. This is no place, however, to indulge in analytical gymnastics over the matter.

ENDOGENOUS FACTORS IN THYROID ACTIVITY

The classical example of an endogenous factor is the congenital absence or functional diminution to ineffectualness of the thyroid gland. The result is an athyreotic individual in the first case and a cretin or human dwarf of a well recognized type in the second (59).

The early ablation of the thyroid from sheep (75) or other experimental animals sometimes, but not always, results in a markedly stunted individual (21). Such specimens should not be called cretins, for the latter, as stated above, result from a congenital developmental defect (65), which produces quite a different picture from that following thyroid removal. The histological studies of Kull (45), Rumph and Smith (71), and others (2) indicate that the fetal thyroid may indeed be functionally active some time before birth in the normal individual. If such be true it is obvious that the congenital absence of the organ would have quite different effects on development than would experimental ablation even in the new-born.

Some observations suggest that hereditary and familial factors may be inductive of disturbances in the level of thyroid activity (42; 46; 17). As far as I know, however, the data have yet to be critically analysed.

SEX AND THE THYROID

Another possibly congenital, but nevertheless real endogeneous factor is sex.

An enlarged thyroid, commonly called a goiter, is a sign of quantitative if not qualitative alteration in glandular activity (4). Old records state and paintings of early artists such as Botticelli attest the fact that a slight swelling of the throat, which we now know to be due to thyroid enlargement, was considered an attribute of beauty. Even a cursory inspection of the early paintings impresses one that this peculiarity was almost exclusively found in women. In modern times recognition of the sex difference in incidence is evidenced in the advertisements for cures of the disorder found in the *Police Gazette* and other like advertisers of spurious proprietary remedies. Here too the caricatured sufferer depicted is always a woman.

This popular impression is borne out by the statistical studies of Marine and Kendall (53), Levin (47) and others. These show that to-day, as always, the incidence of thyroid disturbance is greater in girls and women than in boys and men.

The basis of the difference undoubtedly lies in the difference in the sex physiology and the sex difference in relation of the gonadal incretory activities to thyroid activity (13). It is a well known fact that thyroid enlargement frequently occurs in women during the shifts in ovarian activity associated with menstruation, pregnancy, and the menopause (65). These can justly be considered causal factors of thyroid disturbance, and, being absent in the male, as contributors to the sex difference in goiter incidence. Consistent with this is the fact shown in an analysis of the weight correlations of thyroid and gonads of sexually mature albino rats, that positive association, as mediated by the adrenals, seems to be stronger in the female than in the male (22). Finally, marked sex differences in degree of growth retardation following thyroid removal are found, as will be shown presently.

Thyroid enlargement at puberty is a common occurrence. The peak of the incidence curve of simple physiological goiter is associated in both sexes with this coming into activity of the incretory function of the reproductive system (47). As will be shown later, puberty also conditions a marked change in the reaction to experimental thyroid deficiency.

All these give ample proof that sex factors are endogenous determinants of the level of thyroid activity.

Emotional excitability is also an endogenous factor of influence. Clinical records contain many reports of thyroid enlargement directly traceable to emotional stress (60; 56). This was particularly noticeable during and immediately after the World War (14).

THE INFLUENCE OF DIET

Foremost among the immediate exogenous factors is dietary deficiency. The responsible substance in most cases is iodine (15).

In the consideration of the influence of diet it is necessary to differentiate between the character and the iodine content. McCarrison (49) has recently reported thyroid disturbance dietary in origin and seemingly unrelated to iodine. A vitamin deficiency such as causes scurvy also may affect thyroid function (55). I myself have increased the weight of the thyroids of albino rats from one to two hundred per cent above the usual by giving the animals nothing but meat, and have cut the size to half or less by giving them nothing but lettuce. Thus the character of the diet is of importance (74), although it may be that the reactions will ultimately be traced back to inadequate iodine, that is to say, an iodine ingestion inadequate for the strain put upon the thyroid by the unsuitable diet.

Now a diet deficient in iodine is so because its food-stuffs are iodine poor. The mineral composition of food-stuffs is directly related to the available nutrients in the soil on which they are grown. Therefore the iodine content of the diet is related to the geographical or geological distribution of iodine in the soil and potable waters from which it is derived. Thus geographic location and geologic formation are important factors in determining the level of thyroid activity. These facts have been largely worked out by the painstaking efforts of McClendon (52) and his co-workers. To illustrate the point Figures 1 and 2 from his publications are given. The first represents for the United States the regions of low and high iodine content in soil, water, and food. The second shows the incidence of simple goiter in the same regions. The negative correlation is striking. Such geographic differences are not confined to the United States. Kendall (40) has found that thyroids of abattoir animals in this country tend to be much poorer in the essential element than those of England. These world-wide differences indicate the importance of geographic or geologic factors.

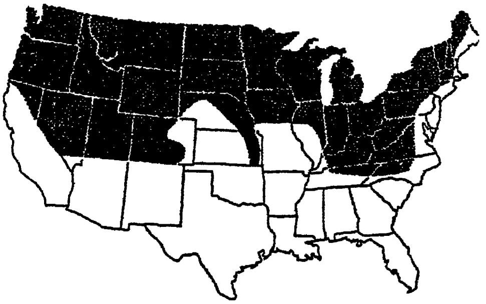

Fig. 1. The Iodine in Drinking Water in the United States

In the black area, waters contain from 1 to 22 parts of iodine per hundred billion parts of water; in the white area, from 23 to 18,470 parts. Courtesy Jour. A. M. A. (From McClendon and Hathaway.)

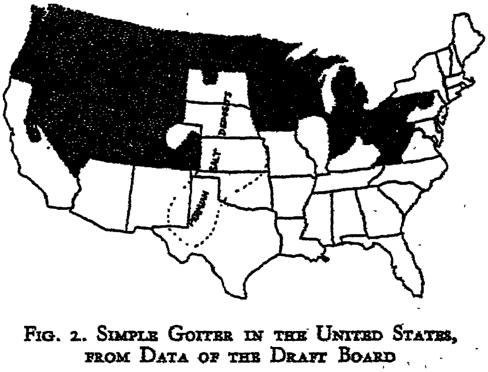

Fig. 2. Simple Goiter in the United States, from Data of the Draft Board

In the white area there were from 0 to 5 military goiters per thousand drafted men; in the black area, from 5 to 111. Courtesy Jour. A. M. A. (From McClendon and Hathaway.)

Allied to the geographic factor is that of climate or season. Seidell and Fenger (72), and Kendall and Simonsen (39) report a definite seasonal variation in iodine content of the thyroids of slaughterhouse animals. Riddle and Fisher (68) found seasonal changes in thyroid size in pigeons. No matter whether these changes are direct reactions or mediated by other endogenous or exogenous influences, the fact remains that season is a factor conditioning the level of thyroid activity.

Finally it has been found that infections and parasitic infestations (1) are frequent exogenous initiators of thyroid disturbance. Though focal infections are suspected, and justly, of stirring up the gland (64), interest has been largely centered on the demonstration by McCarrison (50) and his co-workers (51) of the marked thyroid reaction to intestinal bacterial putrefaction.

THE INFLUENCE OF THYROID FUNCTION ON GROWTH

The environmental factors known to produce changes in the level of thyroid function have thus been briefly sketched. The influences of these changes on growth and development will now be discussed. The literature is appallingly voluminous. It would be an injustice to inflict the printing of the mass of references on this journal. Therefore most of my citations will be to papers in which antecedent studies are reviewed. This implies no lack of recognition of the worth of work not individually cited.

Thyroid activity may either increase or decrease. Each of these changes has an influence upon growth.

When thyroid function is deficient, either by accident as in cretinism, or by design as in experimental ablation, growth is retarded (23). When such stunted individuals are given thyroid, growth is accelerated (66; 76). From these facts as well as from a priori considerations it is assumed that the administration of thyroid by feeding or other means to normal subjects is a valid method of producing in the organism a condition analogous to an increase in thyroid functional level. Such an increase in the initially normal animal may result in either acceleration or retardation of growth (7; 24). The size of the dose administered determines which way the cat will jump. If the amount given does not increase total metabolism to the point where catabolism predominates, growth in weight is hastened. If the amount is large enough to put anabolism in abeyance, so that more energy is expended than can be assimilated, growth is slowed. This reaction occurs whether whole gland substance is used or the crystalline iodine-containing hormone thyroxin (8) first isolated by Kendall (41). Differential organ hypertrophy results from such acceleration in rats and rabbits, though recovery tends to follow the discontinuance of high thyroid feeding (9). These short time experiments serve to show that distortion of bodily proportions is producible by increase in thyroid function.

Alteration of differential development resulting from excessive thyroid activity is not confined to mammals. The studies of Romeis (70), Gudernatsch (20), Swingle (78), Uhlenhuth (80), Drzewicki (11), and others, have well demonstrated the intrinsic importance of thyroid functional level on structural development and allied phenomena in Amphibia, Reptilia and like forms. Metamorphosis can be accelerated, retarded, or inhibited at will according to the experimental procedure used.

In the fowl also, as representative of the family Aves, it has been found that hyperthyroidization produces definite structural alterations (57; 37; 82; 18; 43). Even the Insecta have not escaped the attention of the all-curious scientist in this field (67). But here the data are complicated by the fact that structures analogous to the thyroid have yet to be surely identified in this group of organisms.

In the family Pisces much work has been done with trout by Marine (54). Here, however, the interest has been chiefly in the elucidation of the cause and prevention of the goiter to which the species is susceptible, and but little if any in functional or structural modifications. It should be marked in passing that diet and iodine separately have been found to be factors influencing thyroid size in fish as in other forms.

All these observations attest the ubiquity of developmental disturbance induced by increased thyroid activity.

Lowered thyroid activity, or thyroid deficiency, also has a definite influence on growth. But here gross growth is always retarded. This is because the assimilative processes can only change in one direction when a metabolic stimulus is lessened or withheld. They must decrease. The pace slackens and the growth increment per unit time decreases.

The fact of this growth retardation has been established by countless experiments on many different species of animals. It is an old story in which the characters are many. The parts they have played in the development of the tale is told in my series of studies of the rôle of the thyroid in growth and need not be repeated here.

CHANGES IN DIFFERENTIAL DEVELOPMENT

Of more recent interest is the search for the answer to the question as to whether the growth retardation is accompanied by a distortion of differential development. The answer will be given as written by the thyroidless albino rat (*Mus norvegicus albinus*).

The data to be considered are the growths of the body and organs of the tests in terms of that of their litter mate controls. Male and female animals of six different ages were used, viz. 23, 30, 50, 65, 75 and 100 days at time of thyroid removal. This was done so that a picture of the rôle of the thyroid in growth at different stages of development would be obtained. All were allowed to grow until 150 days of age, when the animals were killed, the organs removed and weighed and the records completed. Basic figures were given by other organ weights from other rats dissected at the ages of initiation of thyroid deficiency. Thus there was made available material for calculation of the growth increment. Males and females were separated at weaning so as to avoid the mating variable and its consequences. All the rats were from the Experimental Colony Stock of The Wistar Institute and had a common inheritance. Controls and tests were kept under identical conditions of diet and environment. Only those tests were used in the final analysis in which no trace of thyroid tissue was found at autopsy. Further details of the technic and the number and distribution of the animals will be found elsewhere (23; 26).

As I wish to discuss the influence of the age of the animal at the time of thyroid removal on subsequent development under the conditions of thyroid deficiency, as well as the effect of this deficiency on differential development, I will present a group of charts from which both relations may be easily visualized. With some modifications these are the same as those published in my final paper in the *American Journal of Physiology* (27). In these figures age is charted on the abscissa, and the percentage increment of the test structure in terms of that of the control on the ordinate. Thus the height of the line above the base at any given age point tells how much less or how much more the structure grew in the thyroidless animal than in the control during the interval between thyroid removal and 150 days of age. The influence of increasing age at time of initiation of the glandular deficiency on subsequent development is ascertained by following the lines from left to right. These are not weight but increment values. A process as well as a condition is being visualized.

Now it would be possible to take any one of the several structures studied as a basis of reference for the inquiry as to whether or not differential development is distorted in conditions of thyroid deficiency. While such a procedure would give the answer, it would make difficult a determination of the reaction of the organism as a particulate entity. As this is a desideratum, body weight has been chosen as the reference base. This is represented in the charts by the heavy continuous line. The growth increments of the other structures as percentages of the normal are given by the lighter or discontinuous lines. As with one exception growth of all the organs was retarded by thyroid deficiency, a line above the body weight base means that the particular organ represented was less retarded than the body as a whole, while a line below indicates the retardation was greater. In many cases growth was not only retarded, it was even rendered retrogressive and weight was actually lost. When this occurs the values become negative and the line dips below the zero ordinate. With this introductory explanation we can now go on to an examination of the data.

An inspection of the charts brings out the fact that the older the animal at time of initiation of thyroid deficiency the greater the subsequent growth retardation. This is not due to the shorter interval for recovery, but is an actual age difference in sensitivity. The conclusion is developed from curves published in another place (26), where it is seen that the initial reaction is less the younger the animal, and that the deviation of the course of growth of the tests from their controls increases with the age of the animal at time of thyroid removal.

This increasing susceptibility to growth retardation with age is attributable to the increasing dominance of growth in cell mass over growth in cell number, and the dependency of the former phase on the anabolic processes, which have been shown to be markedly subject to the level of thyroid activity (63). It is evidence for the conclusion that the thyroid is more concerned in growth by increase in cell size than in growth by increase in cell number.

THE THYROID AS A REGULATOR OF THE METABOLIC RATE

Considerable effort has been expended in the attempt to determine the rôle of the thyroid in cell division. Critical examination of the work of those who claim a specific stimulative influence uncovers a lack of appreciation of the fact that thyroid substance itself contains nutrient material aside from the hormone thyroxine (12; 40; 77). Such uncontrolled results hardly merit conclusion. Careful workers, using adequate control as to dosage and material, have not found much. Carrel in a personal communication writes that "We tried thyroxin on pure cultures of fibroblasts some years ago, only from the point of view of a possible effect it might have on the rate of growth. We have never observed any acceleration. Our results have not been published." Butler (6) came to a like result with eggs of *Arbacia*. Gray and Loeb (19) state that—"administration of thyroid gland substance is not followed by a phase of stimulation, but . . . . within the first two weeks a period of depression sets in . . . ." These authors worked with guinea-pigs and the thyroid was the organ studied. Torrey, Riddle and Brodie (79) showed that thyroxin accelerates certain metabolic processes in *Paramecium*, but does not stimulate cell division. These observations, combined with the well-established facts as to the general metabolic function of the thyroid, justify the conclusion that the rôle of the gland in growth is that of a participant in the regulation of the metabolic rate, through which is determined the level of the maintenance processes of the organism and hence the amount of material presented to the cells for growth purposes during a given period, and that it offers no specific stimulus to growth by increase in cell number.

Thus it is seen that during the period of most rapid growth and up to the time when the curve becomes asymptotic, age is a potent factor in determining the degree of reaction to disturbances of thyroid function.

The charts also show that sex is a factor, for in general, the growth retardation is greater in the female than in the male. The direction of difference is the same as that in normal rats. That is to say, just as the degree of thyroid determined retardation is greater the less the rate of normal growth on age, so is the degree of retardation greater in the female, whose growth is normally less than that of the male. The fact that the sex difference in reaction to thyroid deficiency is correlatable with the sex difference in normal growth shows the interpretation of the age difference in reaction to be well taken.

While the sex (male-female) difference is attributable to sex-inherent differences in general growth capacity, the coming into activity of the sex organs at puberty is another matter. In the one case we are dealing with congenitally determined differences in chromosome constitution with their influence on general growth; in the other we are dealing with the physiological changes due to the influence of gonadal incretory activity. A study of the charts brings out the fact that puberty, which begins in the rat at about 65 days of age, determines a definite shift in the degree of reaction to thyroid deficiency initiated at this time and thereafter.

It is well known that in normal individuals puberty is accompanied by change in growth rate and heightened sensitivity to external influences. It is to be expected that this would be reflected in the reaction to thyroid deficiency. In these investigations the effect is particularly marked in the visceral organs and the thymus (Figs. 5, 6, 7, and 8). Here there is not only a complete inhibition of growth but an actual retrogression or loss of weight. There is no doubt that this is real. It occurs in both sexes.

These pubertal changes are not confined to organ growth. They occur also even in the chemical make-up of the bones (29; 30), blood, and central nervous system of thyroidless animals (31). It is not necessary to make a detailed analysis of the phenomenon. This has been done in earlier papers. All that I wish to point out here is that puberty is an important factor in the determination of the degree of response of the organism to thyroid deficiency.

The analysis of the influence of thyroid deficiency falls into a major and a minor bracket. Of major interest is the answer to the question as to whether differential development is distorted. Of minor interest is the query as to whether the observed differences indicate specific thyroid relationship.

INFLUENCE OF THE THYROID ON THE GROWTH OF DIFFERENT ORGANS

A study of the charts reveals that the organs can be roughly grouped into three classes with regard to their growth retardation relative to that of the body as a whole.

There is the Resistant Group: the eyeballs, brain, spinal cord, body and tail growth in length (Fig. 3), and the long bones (humerus and femur) in both weight and length growth (Fig. 4). The growth of these is in general definitely less retarded than that of the body.

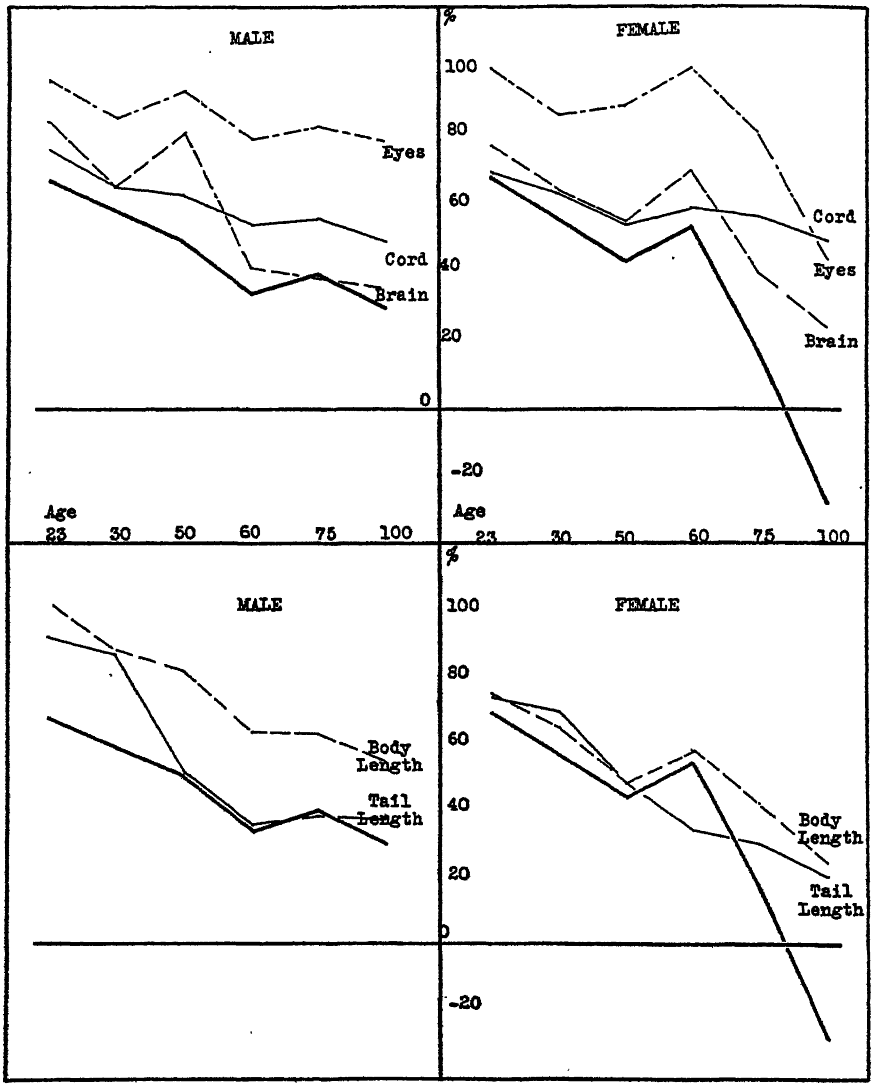

FIG. 3. THE RELATIVE GROWTH RETARDATION OF THE EYEBALLS, BRAIN, SPINAL CORD, BODY LENGTH, AND TAIL LENGTH IN MALE AND FEMALE THYROIDLESS RATS

Reproduction of Figs. 3–9 is made possible through the courtesy of Williams and Wilkins Co., Baltimore

There is the Sensitive Group: the lungs, heart, submaxillary glands, liver (Fig. 5), kidneys, spleen (Fig. 6), adrenals, pancreas (Fig. 7) and the ovaries and uterus after puberty (Fig. 8). The growth of these is markedly more retarded than that of the body as a whole, indeed in many cases it is rendered retrogressive.

Finally there is the Special Group: the testes, epididymis, thymus (Fig. 8), and the hypophysis (Fig. 9).

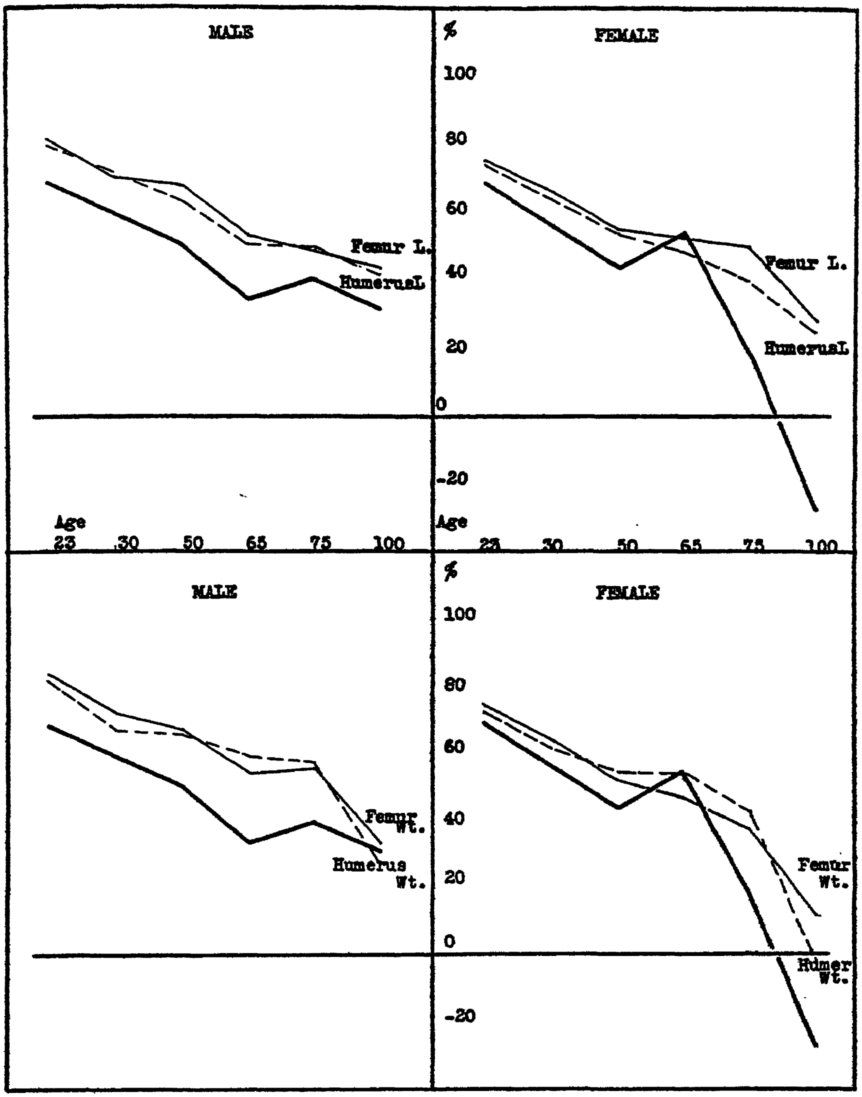

Fig. 4. The Relative Growth Retardation of the Long Bones in Male and Female Thyroidless Rats

The testes and epididymis are set off because their growth is largely determined by their specific function of production and storage of new cells (32). Their high resistance to the growth inhibiting influence of thyroid deficiency is strong support for the idea that thyroid activity is more concerned in growth by increase in cell mass than in growth by increase in cell number.

The thymus is put in the special group because of its exquisite sensitivity expressed as devolution to any nutritional or toxic disturbance (33), and because its function is unknown.

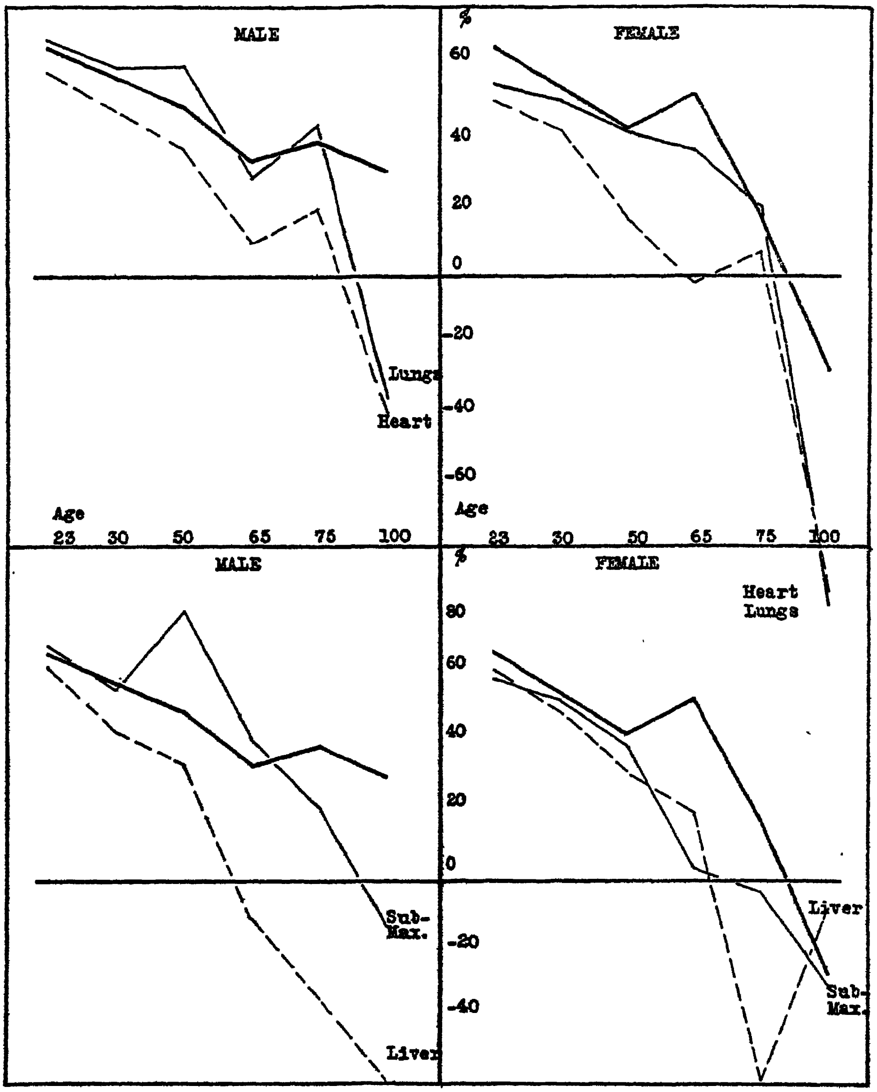

FIG. 5. THE RELATIVE GROWTH RETARDATION OF THE LUNGS, HEART, LIVER, AND SUBMAXILLARY GLANDS IN THYROIDLESS MALE AND FEMALE RATS

The hypophysis naturally falls in the special group because of its well known specific relation to the thyroid (73), which is exhibited in a growth acceleration instead of retardation in conditions of thyroid deficiency.

From these results it is clear that thyroid deficiency produces a distortion of differential development. Because of the difference in degree of retardation exhibited by the various structures, the proportion of the total which they hold as individuals in the normal is changed and the end result is an animal of quite different structural proportions in so far as weight relations are concerned.

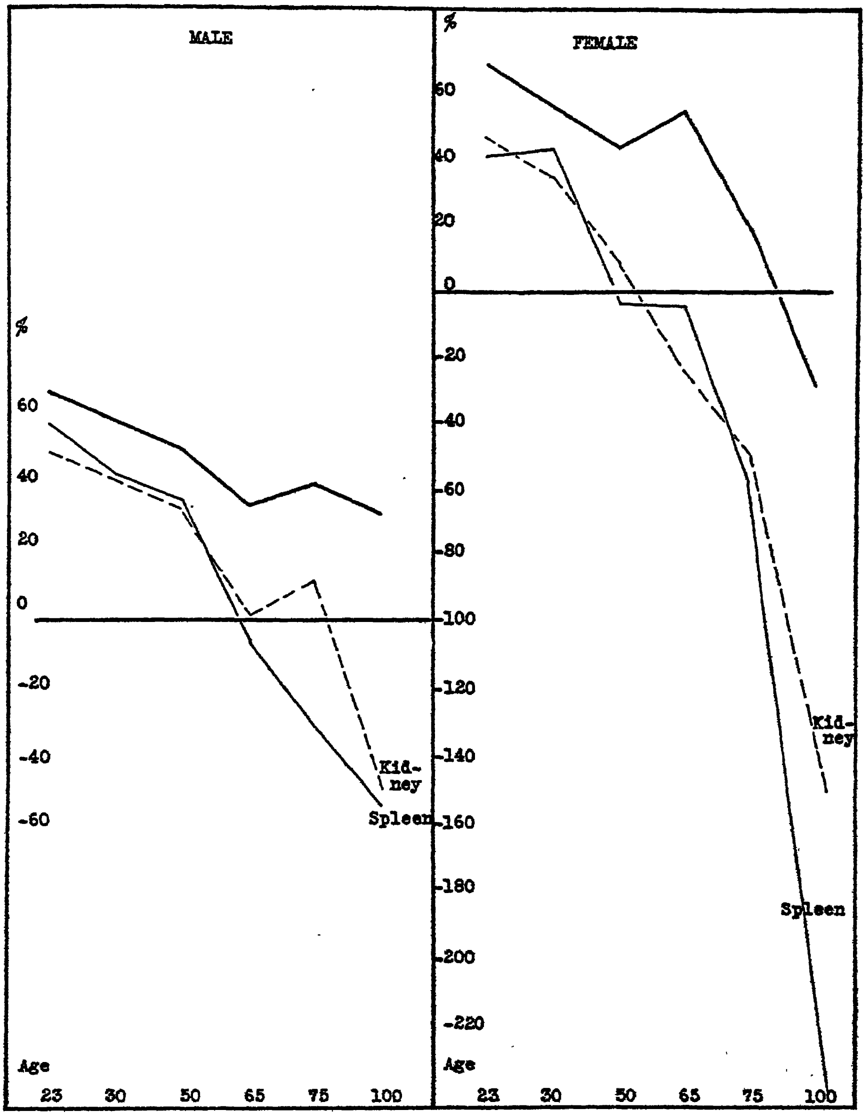

Fig. 6. The Relative Growth Retardation of the Kidneys and Spleen in Thyroidless Male and Female Rats

A further examination of the charts shows that there is a general consistency in the direction of deviation of organ growth development from that of the body as a whole. This holds regardless of the age at time of glandular removal or sex, save for the exceptions which are discussed elsewhere (27). It is additional evidence for the point that a new structural type of individual tends to be produced. The experimental procedures have yielded an animal in which the nervous and skeletal systems are larger and the viscera of smaller proportions than usual of the total body mass.

Other data show that the humerus and femur are longer as well as heavier than is usual in animals of the body weight recorded, and tend to be ever so slightly longer for the body length (35). This combined with the fact that the body length is less retarded than body weight,

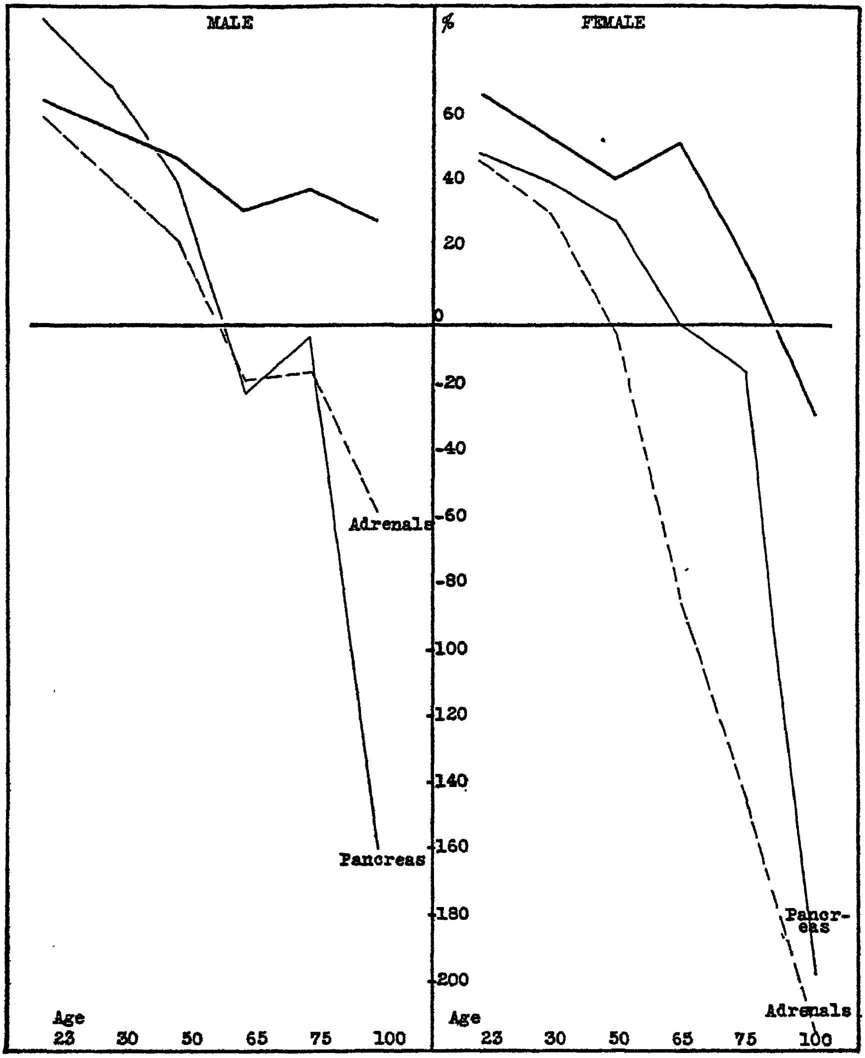

FIG. 7. THE RELATIVE GROWTH RETARDATION OF THE PANCREAS AND ADRENALS IN MALE AND FEMALE THYROIDLESS RATS

indicates that a more slender animal has been produced.

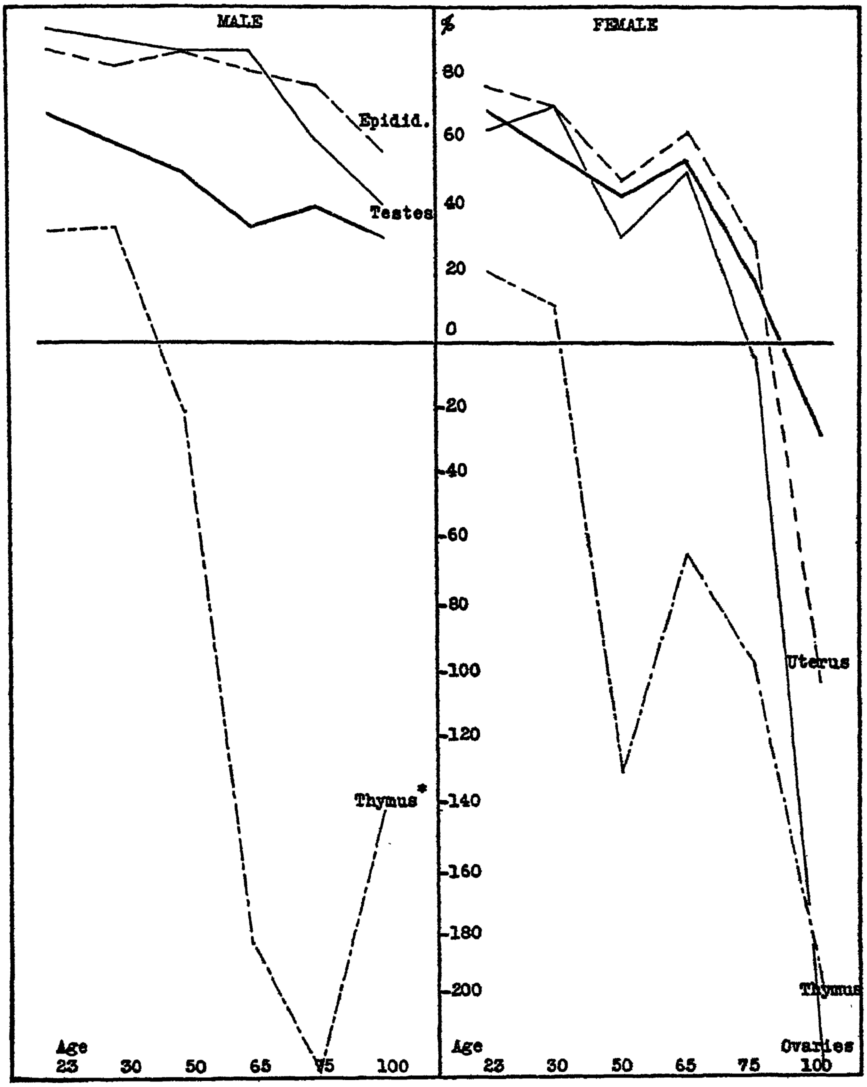

Fig. 8. The Relative Growth Retardation of the Reproductive System and the Thymus in Male and Female Thyroidless Rats

DIFFERENCES OF REACTION OF ORGANS DUE TO ALTERED METABOLIC LEVEL

Now what is the basis of the organ difference in degree of reaction? Is it an expression of a specific influence of glandular activity on the growth of the individual organ, or is it an expression of the difference in relation to the lowered metabolic level of the fundamental characteristics peculiar to the organ?

In the analysis of the rôle of the thyroid in growth the thesis was developed that the growth retardation of the body as a whole which obtains in conditions of thyroid deficiency is the result of an essential undernutrition and not of any specific growth relation to glandular function as such (28). The charts show, with a few exceptions which are explained in the papers dealing with the separate organs, that the trend of the direction of change in degree with change in age at time of glandular removal, is generally the same for the organs as for the body as a whole. It is therefore obvious that the major factor is the dependence of the organs on the growth processes of the body as a whole. The conclusion then is that the reaction is due to specific organ constitution and the relation of this to the metabolic level, rather than to any specific influence of glandular activity on the growth of the individual structure.

It might be thought that the difference in degree of retardation exhibited by the several organs is based on their normal difference in growth rate. A study of the data reveals that this is not so. There is no direct nor reciprocal concordance between the normal growth capacity and that which obtains after thyroid removal when inter-organ comparisons are made.

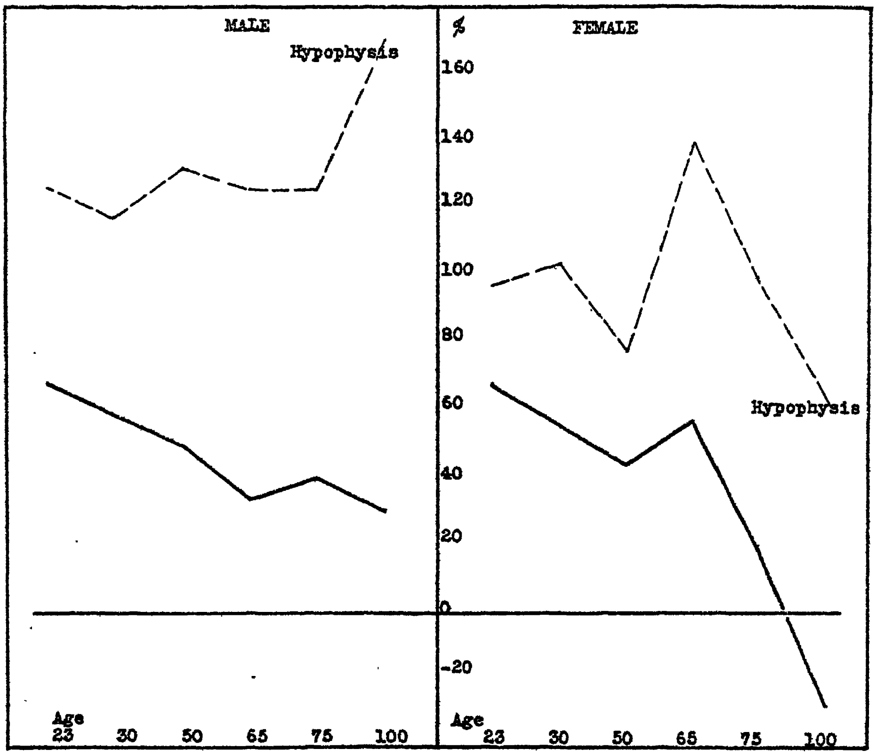

FIG. 9. THE GROWTH ACCELERATION OF THE HYPOPHYSIS IN MALE AND FEMALE THYROIDLESS RATS

Since neither specific thyroid-organ relations nor inherent growth capacity differences are at the bottom of the organ differences in degree of retardation, it is necessary to look elsewhere for the solution.

THE WORK-GROWTH RATIO

Now although growth is retarded, inhibited and even rendered retrogressive, function continues, else the animals would not continue to live. From this it is clear that function transcends increment. In the energy expenditure of an individual organ incident to living a part is used in repair, a part in growth, and a part in the work associated with the specific function. The work-growth ratio is obviously higher in the metabolic organs, the chief functional concern of which is to work over, elaborate, prepare, transport, secrete, or excrete materials for the rest of the body, mainly outside the organ itself, than in those in which no such generalized functional characteristic is exhibited.

Since function transcends increment it naturally follows that with a decrease in energy supply a greater than the usual proportion of what is available is used for work and a lesser than usual for growth. In organs of higher work-growth ratio the relative decrease in energy utilization for growth would be greater than in the organs of lower work-growth ratio. Therefore the former should exhibit a greater growth retardation than the latter. And such is seen to be the case. The metabolic organs: the lungs, heart, submaxillary glands, liver, kidneys, spleen, pancreas, and adrenals are the more sensitive and their growth is more retarded than that of the non-specifically metabolic structures comprising the resistant group: the eyeballs, brain, spinal cord, femur, humerus, tail, back-bone, hypophysis (?), and uterus and ovary before puberty.

THE METABOLIC LABILITY OF THE ORGAN SUBSTANCES

Associated with the functional characteristics is the nature of the characterizing materials incorporated into the organs during growth. The relative metabolic lability of these is of importance. For the more metabolically labile they are the more readily are they utilized in conditions of inadequate nutrition. The organs which tend to lose weight under the growth-retarding influence of thyroid deficiency are just those organs which grow by increments of materials more metabolically labile than those of the resistant structures of lesser work-growth ratio in the metabolic sense. The labile protoplasmic mass concerned in carrying on the specific function of the organ is a larger proportion of the total mass in the sensitive group than in the resistant group. For example, the latter is made up of the skeletal system, characterized by deposits of relatively inert calcium salts; the central nervous system, characterized by relatively stable lipoids in high concentration; the eyeballs, of which the metabolically inert humors are a relatively large part of the whole; and finally the ovary and uterus before puberty, growing by increments of no immediate functional utilizability.

This brief analysis shows clearly that the basis of the organ differences in degree of growth retardation lies in the specific functional and compositional characteristics and the relation of these to the generalized lowering of the metabolic level.

The demonstration of the fact that thyroid deficiency produces distortion of differential development and a trend to a new structural type having been made, and the bases therefor having been outlined, we are now in a position to consider the implications in the light of what is known of the effect of exogenous and endogenous factors on the level of thyroid activity. Such a procedure is acknowledged to be purely and simply a synthesizing speculation. Apologetics are not required. It is a necessary as well as a legitimate part of scientific endeavor to review the prospect presented from the eminence of experimental accomplishment and to sketch the terrain spread to view. The contours are there. Whether they have been viewed myopically, hypermetropically, or with astigmatic distortion is a matter for the future to settle.

THE THYROID AS AN ADJUSTOR OF STRUCTURE TO ENVIRONMENT

As a preliminary it is well to fix in mind the fact of the extreme proclivity of the thyroid to size variation. Common observation suggests and statistical analysis establishes the phenomenon as peculiar. I found that in the mature albino rat the thyroid is the most variable of all the structures studied (22). The degree of superiority is so great that it sets the organ apart as unique. If we assume, as I think we have a right to do, that the size variableness of the thyroid is an expression of a corresponding functional variability, we have in this gland a particular mechanism of exquisite sensitivity through which environmental factors may play a significant rôle in the determination of bodily structure.

The geological record shows that profound climatic and seasonal changes have swept over large areas of the earth's surface during past ages (62). Glacial advance and retreat produced ebbings, flowings, and migrations of flora and fauna. Submergence brought the hinterland to the borders of the sea, while emergence threw up new habitable terrains. Thus have occurred shifts in the relative availability of iodine, the element essential for thyroid activity, and for which the sea is the chief source. As Lyell has postulated, these changes were not catastrophic but gradual in their development and recession. They were spread over hundreds of thousands if not millions of years, during which reproductive activity produced thousands of generations of living things.

The consequent shifts in climate and nature of the habitable areas, which were consistent in one direction for long periods of time, were indubitably factors productive of changes in kind and amount of flora. The faunal migrations and scatterings which were similarly induced brought changes in dietary habits and materials.

From the observational and experimental evidence cited at the beginning of this paper it would seem as if these long time uni-directional shifts in environmental factors must indeed have induced changes in the general level of functional activity of the sensitive thyroid. While the type of change in the organ would be dependent on the type of environmental and dietary alteration, it would nevertheless be consistently in one direction according to the direction of shift in environment, and continuous through countless generations.

On the basis of my experimental data it is not beyond the bounds of reasonableness to conclude that conditions such as described would be reflected in the body as a whole, and would be productive of modifications of inter-structural relations in a particular direction. This is all the more probable when it is remembered that the influence of thyroid deficiency on structural alteration is greatly enhanced by the onset of reproductive function; that the degree of alteration is much greater in the female; and that the reproductive system as well as the reproductive capacity of the female is particularly affected (25). Because of this the offspring in successive generations could hardly be expected to escape reflecting the changing trend of the formative parent.

The logical deduction is that thyroid function may well have been a significant participating factor in the production of varieties within a species if not of species within a genus during the age-long course of evolution of those animal types which possess the gland.

A POSSIBLE MECHANISM FOR THE INHERITANCE OF ACQUIRED CHARACTERS

A further implication is presented.

It is clear that a modification of the relative functional intensity of the several organs is a natural accompaniment of the modification of their weight inter-relationships. This shift can be considered uni-directional since the cause is consistently of the same nature in all groups. Therefore an animal is obtained in which the participation of any single organ in the *totale* of the metabolic processes is different from that normally found. The whole character of metabolism is altered as well as the rate, and altered in one direction.

Now the chromosomes, which are alleged to be the carriers of heritable characteristics, are objects of substance, not ephemeral things, and as such are made up of complexes of chemically simple organic compounds. Bio-physical as well as morphological studies indicate that these compounds are not inert and unreactive, but labile in high degree. It would be strange indeed if the chemical molecules constituting the chromosomes were not subject to chemical alteration by adequate change in the chemical, e.g., metabolic, environment. Such a staticism would hardly be consonant with life. I can see no chemical justification for exempting the germ-cell chromosomes from this principle.

From this premise it follows that adequate chemical agencies could well produce a shift in the nature of the chromosome radicle reaction from which an alteration of offspring character would ensue. It is conceivable that a potentially adequate agency would be a fundamental shift in the character of the metabolic milieu, since the chromosomes, being chemical in nature, are at one and the same time the products of and the contributors to the general type-specific metabolic environment. Note that I write the character, not the degree, for a shift in degree would largely affect the speed and not necessarily the type of reaction.

Now such a shift occurs in conditions of thyroid deficiency. It is therefore possible that the sensitivity of the thyroid to respond by changes in functional level to changes in environment, being continuously brought into play in one direction over long periods of time, might well afford a mechanism through which the inheritance of acquired characters is producible.

The obvious objection to these speculative interpretations is the fact that there are many species of organisms which do not possess a thyroid, and hence what has been written here has but a limited if any significance.

On the other hand it must not be overlooked that the general applicability of the concept is not centered on the thyroid as such but on the thyroid as a factor concerned in the maintenance of the metabolic milieu characteristic of the species possessing the organ. If the basic idea is correct any fundamental distortion of the character of the metabolism (i.e., of its inter-constituental relations) uniform in direction over long periods of time acting through countless generations should be a potentially adequate mechanism whereby varieties within a species, plant or animal, species within a genus, and the inheritance of acquired characters are producible.

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As this goes to press the American Chemical Society's Monograph on *Thyroxine* by Kendall makes its appearance. In this there is to be found the material chosen from the viewpoint of the chemist with respect to the compound designated in the title.

HOW LARGE IS THE MAMMALIAN EGG?

A REVIEW

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IF ONE sketch the outline of a hen's egg so as to fill a page of this Journal as nearly as possible, the egg of the oviparous Australian mammal *Ornithorhynchus*, drawn to the same scale, would be represented by the natural size of the hen's egg, the entire opossum egg with its albumen, by a cross-section of the lead in a pencil, the human egg by a period in average sized type.

Within the phylum *Vertebrata* the differences between the smallest eggs, those of mammals, and the largest is even greater. Thus the eggs of certain "man-eating" sharks (Lamnids) are as much as 220 mm. in diameter. The egg shell of the now exterminated *Apyornis* measured 350 mm. or over a foot in its longest diameter. The ostrich egg is 150 mm. in length and has a capacity of 1.2 liters, or over a quart.

In the evolution of mammals, the Monotremes (*Ornithorhynchus* and *Echidna*) form an interesting link, for they possess in their hairy covering and milk secreting glands the chief distinguishing class characteristics of mammals. Yet they "lay" large yolk-laden eggs from which the young emerge after a short incubation outside the female's body. From the 15-millimeter egg of *Ornithorhynchus* and the 15-millimeter egg of *Echidna* there is a sudden drop to the typical mammalian egg, which measures about one-tenth of a millimeter. It is true that the marsupial eggs show some transitional characters, as for example, the large albumen layer, the shell membrane, and a somewhat richer supply of yolk, as in *Dasyurus* (Hill). But throughout the *Eutheria*, the mammals above the marsupials, the egg is very uniform, with not much over a two-to-one variation in size (table 8), which holds from rat to man, from bat to horse, from mouse to elephant and whale. The size of the animal bears no relation to the size of the egg.

The comparison between the large yolk-laden eggs on the one hand and the human egg or the eggs of most mammals on the other is not fair to the latter group, for these represent only the yolk or "vitellus" of larger eggs. The total diameter of the hen's egg, for example, is due largely to the albumen laid down in the oviduct around the vitellus. The human egg has no such envelope, and this is true of all mammals with the exception of the marsupials and the Lagomorpha (hares and rabbits). Thus the egg of our only marsupial, the opossum, has a thick albumen layer enclosed in a thin shell membrane; the rabbit egg lacks the shell membrane, while all other mammalian eggs have only a highly transparent limiting membrane, or "zona pellucida," which they receive in the ovary before their discharge into the oviduct. The opossum egg, with its opaque white ovum proper in the center of a transparent, hardly visible albumen sphere, looks, in reflected light, much like a grain of sago not quite cooked through—a hyaline sphere with a white spherule in the center.

This comparison between the egg of fowl and that of mammals must be controlled in another way. The yolk or vitellus of the hen's egg is so laden with fat and protein pabulum for the developing embryo that the egg nucleus, with its associated tiny mass of protoplasm, which alone will make the chick embryo, becomes all but lost on the surface of the yolk. But that speck of protoplasm corresponds to the entire Eutherian egg. The reduction in size has, of course, been made possible by the parasitic habit assumed by the mammalian fetus through implantation in the maternal tissues.

In order to visualize for himself the actual size of the mammalian egg, the reader may follow the suggestion which the Berlin anatomist Waldeyer was wont to give his students. Spread out, said he, a sample of sand on a sheet of paper, brush off the easily visible grains and pick out the smallest grain, which it is just possible to see with the naked eye—that speck is of the order of magnitude of the mammalian egg.

THE DISCOVERY OF THE MAMMALIAN EGG

In view of the small size of the mammalian egg, it is not at all surprising that it so long escaped detection. It was not until 1827 that von Baer announced the discovery of the real mammalian and human eggs. From the time of de Graaf (1673) to that of von Baer the large vesicular follicle of the ovary was regarded as the egg. We now know that the ovarian follicles that bear de Graaf's name do not constitute the egg but *contain* the egg. The clear, limpid "graafian" follicles in the ovary of the rabbit, before their dehiscence, do greatly resemble eggs of about eight days' development, but how such large eggs were to pass through the narrow lumen of the oviduct did not, it seems, concern many investigators. I read, however, in Ritchie's interesting book, *Contributions to Assist the Study of Ovarian Physiology and Pathology* (1865) that Morgagni, in his *Adversaria Anatomica Omnia* (1741) made the following reflections: "How much more likely is the conjecture that they (the ovarian follicles) are glands secreting fluid for the purpose of keeping the ovum safe, and helping it to escape when the proper time arrives." The error referred to above was a costly one and doubtless retarded progress in the study of embryology during the century preceding von Baer. It is interesting to note that Jones (1837) varied the error of deGraaf by confusing the gelatinous envelope of the rabbit egg with the liquor folliculi.

However, the century following the "Father of Embryology," the nineteenth, did not produce a large array of investigators who occupied themselves with the study of the early stages of the mammalian egg. Without a doubt the outstanding figure was Bischoff, who published, in the forties and following decades, his classical studies on the rabbit, the dog, the guinea-pig, and other domestic animals, as also the deer. These studies have stood the test of time; Bischoff's measurements on the living eggs were the most extensive up to a very recent date.

My calculations of Bischoff's data are uniformly too high. I have followed Keibel's equivalent of 3 Prussian Inches (P.Z.) the equal of 80 mm. This approximates our equivalent of 25 mm. for one inch. Thus the average given for the dog egg (1845, page 7) is 0.0068 to 0.0070 P.Z. or 1/13 to 1/12 P.L. or 16 to 19/100 mm. These dimensions in micra, according to my calculations would be: 181 to 186, 170 to 184, 166 to 190. It seems that Bischoff attempted exactness only in terms of decimal fractions of the P.Z. (preussischer Zoll.). Since his measurements run pretty uniform though high it is probable that the unit of measurement he used was smaller than he thought by a small fraction.

Sobotta (1895) studied 1459 mouse eggs in maturation and early cleavage, and Long and Mark (1911) 1000 mouse eggs in maturation and fertilization. These constitute the most extensive studies of a single species and on a limited phase of development, but they do not include a single measurement on the living egg. As will be pointed out herein, it is the living egg alone that affords the true picture of the egg as a whole and it is only recently that such studies have gotten under way. This fact does not, however, minimize the fundamental processes in the behavior of the egg which only microscopic preparations can disclose; for stained preparations have taught us about the significant behavior of the chromatin, the chief bearer of hereditary characters.

TABLE 1

From Long and Mark (1911), showing changes in size of the mouse egg during maturation and fertilization, based on eggs fixed in situ

STAGE	NUMBER OF EGGS	AVERAGE DIAMETER IN MICRA
Ovarian:		
Germinal vesicle	109	65.5
Beginning of first maturation division	53	62.5
First maturation division	211	58.0
Tubal:		
Second spindle	507	55.6
Second maturation division	36	53.6
Pronuclei	123	54.0
Eggs in oviduct 16½ hours	50	53.3
Eggs in oviduct 29 hours	50	56.5

SHRINKAGE OF THE TUBAL EGG

Can we state in definite figures, then, with reasonable accuracy, the dimensions of the ovum in each species of mammal thus far studied? Before answering this question we must further define it. In the first place, we must specify the stage of development considered, for manifestly, sooner or later, the egg begins to grow. In this discussion we shall limit ourselves to the one-celled or undivided stage, or at least to the stage of early cleavage. These alone approximate the freshly discharged egg. Now there is considerable evidence in the literature that the nuclear changes of first maturation division in the ovary, the second division, and fertilization after ovulation involve also changes in the size of the egg, even entirely aside from the small mass of cytoplasm and nuclear material extruded with the polar bodies. Long and Mark state that a maximal size of the egg is reached at the end of the so-called period of growth, while the egg nucleus is in the condition of a vesicle. From this time to fertilization there is a progressive slight shrinkage, after which the egg increases in size with its sojourn in the tube. Long and Mark's figures are quoted in Table 1 because they are unique in the number of eggs measured and the care with which the work was done.

TABLE 2

Sizes (in micra) of ovarian and tubal eggs calculated by the present writer from the atlas of van der Stricht (1923) and from his bat paper (1909)

ANIMAL	OVARIAN EGGS	TUBAL EGGS
Man	141×113	
Dog	111×92	102×87
Cat	95×84	81×72
Guinea pig	77×63	63×58
Bat (1923)	95×78	70×65
Bat (1909)	90×69	66×58
Mouse	80×62	53×53

Lams and Doorme (1907) were probably the first to call attention to this phenomenon, which O. Van der Stricht, their teacher, believed to be quite general for mammalian eggs. This author also believed that the low point varies in different mammals, but in view of the condition of the material on which he made his measurements we may well doubt that so nice a point could have been determined by him. That the ovarian egg is generally reported to be larger than the tubal egg there is no doubt, as one can readily see by a study of the literature. Sobotta in 1905 set down the mouse egg at 59 micra for both the ovarian and the tubal stages, but in a later paper he granted 65 to 70 micra to the ovarian, 60 to the tubal ovum. From Van der Stricht's extensive data I have calculated Table 2, from the standpoint of the present comparison. This author's paper of 1923 constitutes a veritable atlas of the early history of the mammalian egg, based on the most extensive and varied series in the world.

A similar excess in size of ovarian over tubal ova I have reported for the opossum, where, however, the former were measured in situ, the latter after being washed from the tube and studied singly. Other data in the literature were mostly based on material fixed and sectioned, usually in situ. The measurements are thus open to objection; both ovarian and tubal eggs should be studied alive in the same medium. This I have done in the case of the rabbit. Ovarian eggs removed from the right ovary, excised surgically seven hours post coitum, measured on the average 122 x 119 micra. Nineteen hours later two eggs were taken from the left fallopian tube; they were in the two-celled stage when removed, but divided again and were four-celled before they could be photographed. They measured 124 x 124 micra, a little larger than the ovarian eggs. Dr. W. H. Lewis killed a rabbit ten hours post coitum, when some of the eggs had been shed while others were still retained in the follicles. One ovarian egg measured 119, the other 133 micra; the average for tubal ova was 124 micra. The progressive changes in size of the mammalian egg, therefore, await more extensive study. This will be made by better methods in connection with other studies on the egg.

SHRINKAGE DUE TO FIXATION

The size changes incident to the vital activities of the developing egg, as set forth above, become insignificant when compared with the shrinkage caused by fixing agents and the after-treatment used in making microscopic preparations. Hence we must know under what conditions the eggs are measured. Since the introduction, about 1870, of the paraffin method of section cutting, by which an egg one-tenth of a millimeter may readily be cut into ten or more sections of convenient thickness, the tendency to use the method on all occasions has been overdone, for it has been substituted for the older and, for some purposes, better method of studying the object in the living state. Refined technique has often been made an end in itself, rather than an aid. Fixing fluids, too, cause a variable amount of shrinkage, those containing osmic acid the least of all. The rate at which the reagents are changed is another important factor. With the most careful treatment the writer kept the shrinkage down, for the most part, to about 15 per cent; more speed in handling the material would certainly have resulted at times in a 30 per cent shrinkage, which is not unusual in much of the work published on the mammalian egg. The study of the mouse egg might be cited in this connection. Sobotta (1905) gives 59 micra for the average mouse egg fixed in either ovary or tube, but in a later paper states that 65 to

70 micra is nearer the truth for the ovarian egg. Kirkham (1907), basing his measurements on the living egg, gives 80 micra for the ovarian, 73 to 78 for the tubal egg. The writer recently photographed five ovarian eggs of a field mouse (sp. ?) and these averaged 95 micra in diameter. It is therefore evident (and on this point there is no disagreement among the authorities) that the fixed egg is no criterion of normal size of the living, functioning egg.

TABLE 3

Measurements made from photographs of mammalian eggs taken in the living state. Negatives on file at the Carnegie Laboratory of Embryology, Baltimore. Diameter of ovum proper (vitellus) or inner diameter of zona. Dimensions in micra

ANIMAL	STAGE	NUMBER OF EGGS	AVERAGE SIZE	INVESTIGATOR
Rabbit	1–4-celled	6	126	Gregory
	Early cleavage	22	124	Lewis
	Ovarian	1	119	Lewis
	Ovarian	1	133	Lewis
	Ovarian	5	120	Hartman
	2–4-celled	2	124	Hartman
Mouse	Ovarian	5	95	Hartman
Dog	1-celled tubal	3	120	Hartman
Pig	1-celled tubal	4	111	Heuser and Streeter
	Cleavage	8	121	Heuser and Streeter
Opossum 56	1-celled tubal	2	145	Heuser and Hartman
313	1-celled tubal	2	126 x 106	Heuser and Hartman
351	1-celled tubal	11	108 x 100	Heuser and Hartman
336, 337	Cleavage	6	151 x 140	Heuser and Hartman
842	Early tubal	7	157 x 152	Hartman
833	1-celled tubal	2	173	Hartman
766	Uterine	1	141	Hartman
Various litters of opossum	Uterine	100	155	Hartman

A further complication is encountered if one attempts to calculate the size of eggs from authors' illustrations where the magnifications are indicated. Articles that fail to indicate magnifications are, of course, of no avail for the purpose of this study (e.g., Rein, Melissinos). Were we to refrain entirely, however, from making calculations from the illustrations in the literature, there would remain jolly little data. The proneness of authors to let the reader make the calculations for himself is illustrated by Van der Stricht's invitation (1923, page 279): "I shall not speak further about the exact dimensions of the eggs [he had not yet given any 'exact dimensions']—it is easy to calculate them from the drawings." This invitation I have accepted, as did Corner (Cowdry's "Special Cytology," volume II, page 1112). The results must, however, fall somewhat short of the true diameter of even the fixed egg, for sections are selected that pass through features of interest, namely the egg nucleus, division spindle, and polar bodies. If these landmarks happen to fall in the middle section of the series the section fairly represents the actual size of the egg; if, on the other hand, the section is a tangential one, the egg is actually larger than the section shows it to be. It is therefore apparent

TABLE 4

Eggs (vitellus only, or inner diameter of zona) measured in prepared sections of fixed ovaries. Sizes in micra

ANIMAL	AUTHORITY	MAXIMUM	MINIMUM	AVERAGE	REMARKS
Dasyurus	Hill, 1911	270 x 260	280 x 126	240	Stated
Didelphis aurita	Hill, 1918	—	—	142 x 129	Stated
Didelphis virg.	Hartman, 1919	185 x 150	—	—	Stated
Armadillo	Newman, 1912	—	—	53	Calculated
Mouse	Sobotta, 1895	—	—	59	Stated
	Sobotta, 1908	70	65	—	Fleming fix., stated
		63	59	—	Bichrom. fix.
	Gerlach, 1906	71 x 55	53	63 x 54	Calculated (few eggs)
	Kirkham, 1907	—	—	71 x 64	Calculated (2 eggs)
	Lams and Doorme, 1907	—	—	68	Osmic fix., stated
		—	—	62	Non-os. fix., stated
	Long and Mark, 1911	77	50	59	Cf. Table 1
	Van der Stricht, 1923	93 x 64	67 x 60	80 x 62	Cf. Table 2
	Kremer, 1924	75 x 75	65 x 55	70 x 70	Calculated
Rat	Kirkham and Burr, 1913	77 x 72	65 x 55	69 x 63	Calculated
	Sobotta and Burckhard, 1910	65	60	—	Stated
	Kremer, 1924	63 x 55	45 x 45	53 x 47	Calculated
Guinea-pig	Rein, 1883	—	—	84	From Lams, 1913
	Lams and Doorme, 1907	—	—	83	Osmic fix., stated
		—	—	79	Non-osmic fix., stated
	Rubaschkin, 1905	92 x 88	80 x 75	89 x 78	Calculated from figures!
		60	55	—	Stated by author!
	Lams, 1913	—	—	80	Fleming fix.; calculated
				70	Non-osmic fix.; calculated
	O. Van der Stricht, 1923	87 x 60	67 x 60	77 x 63	Cf. Table 2
Dog	O. Van der Stricht, 1923	123 x 87	95 x 80	111 x 92	Cf. Table 2
Cat	R. Van der Stricht, 1911	180 x 98	111 x 90	—	2 eggs; calc.
	Longley, 1911	92	79 x 74	—	Calculated
	O. Van der Stricht, 1923	100 x 90	87 x 81	95 x 84	Calculated
Ferret	Robinson, 1918	133 x 116	98	110	Calculated
Horse	Hartman	—	—	135	Carnegie collection (in toto prep.)
Bat	Van Beneden and Julin, 1880	113	90	104	Calculated
	O. Van der Stricht, 1909	110 x 105	50 x 44	95 x 78	Many eggs; calculated
	O. Van der Stricht, 1923	97 x 70	81 x 67	90 x 68	3 eggs; calculated
Human	Nagel, 1888	199 x 194	170 x 165	—	2 eggs (with zona)
	Waldeyer	—	—	130	1 egg
	Bumm (Gynecology)	—	—	200	Stated (with zona)
	Kölliker (Grundriss)	—	—	200	Stated (with zona)
	O. Van der Stricht, 1905	157	120 x 110	140 x 121	Calculated from 13 figs.
	O. Van der Stricht, 1923	179 x 103	107 x 92	141 x 103	Calculated 4 eggs
	Hartman	—	—	120 x 110	1 egg (Carnegie)
Monkey					
(*M. nemestrinus*)	Selenka, 1903	—	—	Ca. 40	Stated
(*M. rhesus*)	Hartman	108 x 100	105 x 90	110 x 93	Carnegie Coll.
Gibbon	Hartman	—	87 x 80	—	1 egg (Carnegie Coll.)
Gorilla	Hartman	—	—	90 x 87	1 egg (Carnegie Coll.)

TABLE 5

Tubal ova studied in sections after fixation, either in situ or after first being removed from the tube. Starred in the latter case. Size in micra (vitellus or true ovum only)*

ANIMAL	AUTHORITY	MAXIMUM	MINIMUM	AVERAGE	REMARKS
Didelphis (opossum)	*Hill, 1918 (*D. aurita*)	170 x 150	112 x 100	126 x 117	Cleavage; calculated
	*Hartman, 1919 (*D. virg.*)	148 x 125	102 x 76	122 x 104	Stated
Hedgehog	*Fischer, A.	46 x 40	—	—	One 3-celled egg; calculated
	Baumeister, 1913	—	—	69 x 54	One egg; calculated
Mole	Heape, 1886	159 (?)	120	125	Calculated
Mouse	Sobotta, 1895, 1898	—	—	59 to 60	Stated
	Lams and Doorme, 1907	—	—	63	Osmic fix.; stated
		—	—	57	Non-osmic fix.; stated
	Gerlach, 1906	68 x 55	48 x 41	60 x 48	Many eggs
	Anikiew, 1908	60 x 58	—	—	Calculated
	Long and Mark, 1911	—	—	55	Cf. Table 1
Rat	Sobotta and Burckhard, 1910	60	55	—	Stated and calculated
	Kirkham and Burr, 1913	67 x 63	55 x 53	61 x 57	Calculated
	Huber, 1915			70 x 62	Few eggs
Guinea-pig	Lams and Doorme, 1907			69	Osmic fix.; stated
				65	Non-osmic fix.; stated
	Rubaschkin, 1905	90 x 74	72 x 58	82 x 67	Calc. from figures × 530
		60	55	—	Stated
	Lams, 1913	60	45	55	Calculated
Rabbit	*Assheton, 1894	145	130	133	Calc. 7 figs. × 165
	*Nihoul, 1926	96 x 92	86 x 80	91 x 83	Calc. Benda fix.
Dog	*O. Van der Stricht, 1923	117 x 103	83 x 70	102 x 87	Calculated; cf. Table 2
Cat	R. Van der Stricht, 1911	114 x 100	89 x 75	105 x 93	Calculated
	Bonnet, 1897	—	—	100	1 egg calc.; Fleming fix.
	Bonnet (text), 1922	—	—	111 x 106	1 egg calc.
	*Longley, 1911	—	—	99 x 81	Calculated
	Hill and Tribe, 1924	90 x 80	69 x 57	82 x 70	Stated
Sheep	*Assheton, 1898	123	105	114	Calculated
Pig	*Assheton, 1898	116	81	100 x 95	Calculated
Deer	Keibel, 1901	115	111 x 106	113 x 108	Calculated
Bat	Van der Stricht, 1909	83 x 73	60	70 x 65	"Selected as typical"
	Van der Stricht, 1923	97 x 70	54 x 53	73 x 62	Cf. Table 2
	Hartman			87 x 73	Carnegie Coll.; 1 egg
Tarsius	Hubrecht, 1902	82 x 70	72	77 x 71	Calculated
Monkey (*M. nemestrinus*)	Selenka, 1903	—	—	40	4-celled

that measurements based on even the best fixed material, especially that fixed in situ, fall short of the actual size of the living egg. This is entirely aside from the irregular shapes which the eggs assume when fixed in situ. I have seldom seen a nicely rounded egg fixed and prepared in the fallopian tube of any animal and I presume that Sobotta had the same experience. Nevertheless this author, by "artistic license," pictures his specimens in what he considered their normal rounded shape. His drawings are the illustrations of maturation, fertilization and cleavage of the mammalian egg most used in the embryological textbooks of all countries.

TABLE 6

Sizes of eggs removed from ovary and measured in living state. Sizes in micra. Vitellus only. (See also Table 3)

ANIMAL	AUTHORITY	MAXIMUM	MINIMUM	AVERAGE	REMARKS
Ornithorhynchus	Gatenby and Hill, 1924	4.4 x 4.16 mm.	—	—	4400 micra
Ornithorhynchus	Caldwell, 1887	2.5 mm.	—	—	2500 micra
Echidna	Caldwell, 1887	3.0 mm.	—	—	3000 micra
Mouse	Kirkham, 1907	—	—	80	
Guinea-pig	Bischoff, 1852	—	—	75	Calc. from figs. × 350
	Reichert, 1861	—	—	87	Calc. from figs. × 320
	Rein, 1883	—	—	65	Calc. from 1 fig.
Rabbit	Bischoff, 1842	182	142	161	Stated (1 P.Z. = 25 mm.)
Dog	Bischoff, 1845	190	166	—	Stated
	Bischoff, 1844	166	160	—	Stated (from polyov. foll.)
Cat	Krause, 1838	170	120	144	Six eggs; calculated
	Longley, 1911	130	105	—	Stated
Goat	Krause, 1838	185	120	—	3 eggs; calculated
Pig	Bischoff, 1844	140	111	—	Several eggs
	Lowery, 1911	157	—	—	"Largest of many"
Bat	Van Beneden and Julin, 1880	—	—	105	1 egg
Macaque	Krause, 1838	140	92	118	3 eggs

THE STUDY OF THE LIVING EGG

What were perhaps the beginnings of a new method in the study of the mammalian egg were made in 1918 by Dr. C. H. Heuser, who, with the writer, under the auspices of the Wistar Institute, made a large collection of opossum eggs at the University of Texas. Many batches of eggs and embryos were at that time photographed in physiological salt solution immediately after removal from the animal. With the assistance of Dr. Heuser, at the Carnegie Laboratory of Embryology, many remarkable photographs of the living rabbit egg in cleavage and germ-layer formation have been secured by Dr. P. W. Gregory and others, and negatives of the early stages of living eggs of other mammals are rapidly accumulating. Indeed, at this laboratory Dr. W. H. Lewis is doing pioneer work in the cinematography of the developing rabbit egg, as he is combining tissue culture with motion picture technique. He has thus far succeeded in keeping the egg alive in rabbit blood plasma for over a week and photographing its normal development for over four days—that is, through cleavage and the formation of the segmentation cavity. The observer may see the entire process before his eyes in a few minutes and much may be learned which would absolutely escape notice by other methods.

TABLE 7

Tubal ova studied in the living state. Sizes in micra. Measurements of ovum proper or vitellus only, or in a few cases, chiefly early cleavage stages, inner diameter of zona. See also Table 3

ANIMAL	AUTHORITY	MAXIMUM	MINIMUM	AVERAGE	REMARKS
Platypus	Burrell, 1927	3.0 mm.	—	—	Whole egg 17 x 14 mm.
Echidna	Simon, 1894	—	—	—	Whole egg 16 x 13 mm.
Dasyurus	Hill, 1911	300 x 290	—	250 x 240	Stated
Opossum	Hartman, 1919	157 x 152	108 x 100	130 x 123	Stated
Hedgehog	Keibel, 1888	120	—	110	(In toto in OsO_4); stated
Mouse	Kirkham, 1907	78	73	—	Stated
Rat	Bischoff, 1844	—	—	100	One egg; stated
	Kirkham and Burr, 1913	—	—	79	Stated
Guinea-pig	Bischoff, 1852	106	91	—	Stated (3 P.Z. = 80 mm.)
	Bischoff, 1852	74	70	72	Calc. from figs. × 350
	Bischoff, 1852	—	—	75	After Lams
	Reichert, 1861	—	—	87	After Lams
	Hensen, 1876	82	65	75	Calc. from sev. eggs
Rabbit	Bischoff, 1842	180	139	160	Stated.
	Costl, 1834–1849	—	—	120	Calculated
	Hensen, 1876	—	—	103 x 93	Calc., 1 fig.
	Grèwsdew, 1896	144	120	133	Calc., sev. figs.
Dog	v. Baer, 1827	—	—	144	"1/15 of a line"
	Bischoff, 1845	174	125	145	"3 P.Z. = 80 mm."
	Hartman	—	—	120	Carnegie Coll.
Cat	Longley, 1911				Cf. Table 3
	Hill and Tribe, 1924	153 x 136	119 x 110	130 x 119	6 eggs in osmic fix.
Sheep	Bischoff, 1844	—	—	140	1 egg; stated
Deer	Bischoff, 1854			115	Stated
Pig	Corner and Amsbaugh, 1917	145	135	140	14 eggs, 3 litters
	Heuser and Streeter, 1928	131	116	121	10 eggs, 3 litters
Bats (spp.)	Van Beneden, 1911	95	86	91	2 eggs (118, 108 with zona)
Monkey	Corner, 1923	86	83	—	2 eggs, degenerating
	Allen, 1927	104	87	—	2 eggs, degen.
	Allen, 1928			104	1 egg, degen.
	Hartman	—	—	107	1 egg, degen.
Human	Allen, *et al.*, 1928	184	117	132	With zona

Photography thus applied to embryology may therefore be expected to yield valuable results. Certainly, from negatives the size of the eggs may be calculated at one's leisure. In Table 3 I have given a number of measurements, chiefly of the opossum egg after photographs taken in Texas and of the rabbit egg after photographs taken by Dr. Gregory and Dr. Lewis.

This section on the measurement of the living egg must not be closed without mention of an event of the greatest significance; namely, the discovery of the first human tubal ovum by Edgar Allen and associated surgeons (Dr. Pratt of Detroit and Drs. Newell and Bland of St. Louis). Seven eggs were recovered from

TABLE 8

Interpretive table, giving the reviewer's estimate of the true average size of the egg of various species of mammal thus far studied. Studies on the living egg are considered the more authoritative and due correction is made for data based on fixed eggs. Dimension of vitellus only. Jenkinson (1913) probably gives size of entire egg

ANIMAL	MOST PROBABLE SIZE OF EGG IN MICRA	JENKINSON'S TABLE
Monotremata		
Platypus	2.5 mm.	
Echidna	3.0 mm.	
Marsupialia		
Dasyurus	240	280
Didelphis	140–160	130
Edentata		
Armadillo	80	
Cetacea		
Whales	140	
Insectivora		
Mole (Talpa)	125	90
Hedgehog (Erinaceus)	100	60
Rodentia		
Mouse	70–75	60
Rat	70–75	
Guinea pig	75–85	80
Lagomorpha		
Rabbit	120–130	150
Carnivora		
Dog	135–145	180
Cat	120–130	
Ferret	120	
Ungulata		
Horse	135	
Sheep	120	150
Goat	140	
Pig	120–140	
Cheiroptera		
Bat	95–105	
Lemurs		
Tarsius	90	
Primates		
Gibbon	110–120	
M. rhesus	110–120	
Gorilla	130–140	
Man	130–140	

six women. The measurements were made on the fresh eggs and are given in Table 7. Previously Corner (1923) and Allen (1927) had recovered eggs from the monkey. These were also measured before fixation (Table 7). The egg of *Macacus nemestrinus*, in the four-celled stage, was studied by Selenka (1903) in the fixed tube and measured in the shrunken state only 40 micra. These cases mark the beginning of the study of the earliest tubal ova in Primates.

THE SIZE OF THE MAMMALIAN EGG

We now return to the original question, How large is the mammalian egg? The reflections set down in this review force the conclusion that for no species of mammal is there agreement on measurements of the egg. Those reported have a range far in excess of variations in the normal living egg, great as these variations undoubtedly are. Perhaps the smallest and the largest of a given species, that is, the extremes in size range of living eggs, are not viable. But we know nothing about this problem; it is one that only tissue-culture methods can solve. The reviewer has therefore thought it desirable to bring together the data contained in the world's literature (at least in that major portion available to him) on the size of the mammalian egg and to present it for what it is worth. If the figures are unsatisfactory the study will serve to emphasize the need of further work and more careful methods than those employed in respect to the making of measurements in the past. For the convenience of the reader the data have been condensed into Tables 4, 5, 6 and 7, classified according to the headings of the tables. As a summary of the whole the writer has been bold enough tentatively to put down in Table 8 his own ideas as to the normal range of the average or modal egg size for the various species of mammals. The table is based first on the best measurements of the living egg and second on an evaluation of the data given by the various authors, due correction being made for the methods used. The table should, however, be regarded merely as a basis for revision in the future. Nevertheless, a perusal of the figures will show that Van der Stricht was probably right when he stated the human egg to be the largest, that of Muridae the smallest among the mammiferous animals. It is also apparent that the smallest eggs are probably not as small as the former estimates would have them, the largest not as large as previously stated. The mouse egg is nearer 70 than 50 micra, the human egg nearer 150 than 200. In other words the table has a tendency to level up the differences in the sizes of mammalian eggs.

Finally it is hoped that the appended literature list will prove helpful to those studying the mammalian ovum for the first time. Studies on the ovum just before and just after its discharge from the ovary were, of course, considered the essential studies. Others might have been added which give sizes of the ovarian egg incidental to histological studies on the ovaries; but it is believed that the list includes a sufficient number of these. The list of papers and books on tubal ova, practically all of which have been consulted by the writer, is believed to be fairly complete.

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SYSTEMATIC BIOLOGY AND THE MUTATION THEORY

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THERE are certain phases of biological investigation which begin with an inquiry into the numbers and the distinguishing characteristics of the different kinds of plants and animals. They continue with an attempt to arrange these kinds of organisms into a classificatory system. They end with an attempt to apply the data thus accumulated to various problems, some of which may be approached only by this very round-about method. All of these activities may be grouped under the general term of "Systematic Biology."

The older theories concerning the processes of evolution were very largely the product of the activities of those who were wholly or in part systematists—witness Darwin's monograph of the Cirripedia—or whose thinking was of the type peculiar to those trained in that particular school. The current theories are increasingly the product of those who are primarily of the experimental or physiological schools and these in their turn are already beginning to give way to those who are primarily chemists.

With such differences in background it is inevitable that there should be differences in the conclusions to which the members of these various groups are led. These conclusions come at times quite sharply into conflict. Matters which from the point of view of one group may seem quite simple become, from the point of view of another, extremely dubious, with such simplicity as they may appear to possess ascribable rather to the minds of those holding the opposite view.

These differences of opinion are perhaps most sharply marked in connection with one particular problem, that of the method of evolution. There are doubtless those among the most modern of all biological groups—the biochemists and the biophysicists—who will not hesitate to yawn audibly at the mention of this problem, just as members of the somewhat less modern groups of experimentalists and geneticists are prone to indicate their boredom with the systematist who talks about "species." It may very well be that all of our speculation as to the mode of evolution is fruitless and that eventually it will rest with the colloid chemist to tell us whether evolution is even a physical possibility and if so how it can have come about.

Pending that time, however, there are still biologists who are interested in speculating about this problem, and its literature grows at a rapid pace. The matters that I wish to discuss here are little side issues of this major problem and have to do with some questions that have arisen concerning the validity of certain assumptions upon which systematists, consciously or unconsciously, base their conclusions. Systematists in the past have contributed to the development of the theory of evolution. In turn that development has influenced the work of systematists. It is proper to inquire what the reaction of the newer theories upon the work of the systematist may be. It is proper to inquire into the basic assumptions of such work and to speculate on the question of whether they check with these newer theories. If not, it is also proper to speculate upon the meaning of the discrepancies.

THE ASSUMPTION THAT CLASSIFICATION EXPRESSES PHYLOGENY

In the pre-Darwinian period, as has many times been pointed out, systematic biology rested upon certain assumptions which are now discarded. It was assumed—quite automatically and almost certainly without any thought that an assumption was being made—that all the species of organisms had been created at one time and that they had remained fixed and immutable since that time. Consequently the "species" was a perfectly fixed and definite thing. It was an actual entity, capable of being placed in a definite pigeon-hole where it would for all time rest in peace and comfort. On this basis, classification, or the attempt to arrange these species into some sort of system, could be nothing more than an attempt to express degree of apparent resemblance. To it there could be attached no deeper significance.

But with the general acceptance of the theory of evolution this condition changed, although it so happened that the nomenclatorial mechanism that had been developed under the previous régime remained to do duty under the new, thus giving some semblance of continuity between the two opposing ways of thought. If species evolve, if they change one into another, then they can no longer be placed in such pigeon-holes, or if they are so placed they may not long be permitted to rest in peace. They must recurringly be dragged out of their repose and bedeviled with questions as to their claims for recognition. Particularly will this be true if evolution has actually taken place by way of a gradual molding of one species into another by means of slow and cumulative changes.

Necessarily the philosophy of classification changed at the same time. Theoretically at least it became something more than an attempt to express merely degrees of resemblance. It became an attempt to express phylogeny, to record the history of evolutionary development. The various taxonomic categories have been assumed to indicate degrees of "blood relationship." This assumption expresses itself graphically in the familiar "family trees."

All of this in theory. Actually, perhaps, the work of systematists has conformed in but a small measure to this theory. Morgan (3, p. 43) remarks,

> A few students of the subject still attempt to arrange their species in such a way as to indicate their relationship by descent, but the attempt, while desirable from the standpoint of evolution, has proven so difficult that it has been tacitly abandoned or ignored by many taxonomists.

And Hall (2, p. 4) has said, "It must be admitted, however, that the spirit of phylogeny is not evident in a large proportion of the revisions and monographs of the present day." After all, only a small proportion of the workers in any particular field are likely to be philosophically inclined. The majority are content, perhaps necessarily so, to perform the task immediately before them without considering its philosophical implications, thus undoubtedly saving themselves from a large amount of worry. Certainly the majority of systematists have been content to name species without troubling themselves very much about the question of whether their "species" were an expression of a definite biological fact or merely of a variable subjective concept. And they have proceeded to group these "species" into genera—or increasingly to isolate them into monotypic genera—and to unite these genera into larger groups without pondering very deeply as to whether they were expressing their phylogeny or were merely putting them together because they look more or less alike.

That the problem bristles with difficulties can not be denied. Consequently it is not to be expected that attempts to reconstruct the phylogeny of any group will be correct in anything more than a broad way. It would obviously be impossible to say of any particular organism, either fossil or living, that it was the actual ancestor of any other organism or group of organisms unless we actually had observed the birth. Lacking such observation we can at the best merely say that there is a strong family resemblance which indicates a probable connection.

Furthermore, even if we had the actual evidence which is necessary positively to demonstrate the phylogeny of all organisms we should still not be free from our difficulties.

If evolution has really taken place by any of the methods which seem at all acceptable, then the number of steps involved in the racial history of any organism from the beginning of life to the present time must be almost infinite. And with a knowledge of those steps we should still have the problem of condensing this history into the limits of a usable classificatory system. The mere mechanical problem of devising such a system would not be small. The degree of compression and distortion which would result might easily be so great as to obscure the facts. Like the so-called "biogenetic law" with its assumption of the compression of the racial history into the embryonic life of the individual, the best that might be said is that some times it seems to have a certain significance.

Nevertheless, if systematic biology is to hold fast to any sort of basic philosophy it would seem that it must hold fast to this. Without at the least the hope that it may express some deeply underlying truth it becomes reduced merely to the accumulation of disconnected and irrelevant facts. That much of systematic work is indeed nothing more than this may, unfortunately, be true, but this does not necessarily imply that there are no other possibilities.

THE ASSUMPTION THAT CLASSIFICATION EXPRESSES DEGREE OF RELATIONSHIP

If we assume that the systematist is attempting to chart the course over which an organism has come during the unfolding of its racial history we may—or at least do—assume that the various categories of our system express also the varying degrees of relationship of this organism to others. Such an assumption is generally accepted by systematists as more or less an axiom.

Let us consider what is meant by the term "relationship" as it is used in such a connection.

In ordinary practice we consider individuals to be related to each other if they have had a common somatic ancestry and we measure the degree of their relationship by the *number of generations* that have intervened between these individuals and the point at which their ancestries merged into a common soma.

As the term is used in systematic biology there is also something of this implication of eventual merging into a common soma, although with modifications. Whether the "ancestor" involved was an individual or pair of individuals or whether it was a group of individuals—a species—would depend upon whatever theory as to speciogenesis we might adopt. And however that may be, there is the further difference that relationship is not measureable by the number of generations that have elapsed. Except in the case of the pedigreed stock of the geneticist, we know nothing whatsoever of the number of generations that have intervened between any two points and consequently the systematist can not be thinking of any such matter when he speaks of the relationship of two groups.

That this is so can be made perfectly clear. We have at the present time living Brachiopods belonging to a group that originated at least as early as the Paleozoic, but which have come down to us practically unchanged from that time. We speak of these as "closely related" to the fossil forms of the Paleozoic. The mammals presumably originated in the Mesozoic, but the mammals of today are very different from any of the earliest members of the group and are consequently not regarded as closely related to any of these ancestral forms. Yet the difference in number of generations intervening between the present day members of the two groups must be inconceivably great.

Evidently then "degree of relationship," as understood by the systematist, means only the degree to which there is a common possession of anatomical characters and the degree of development of those characters. Thus, those forms which agree in the common possession of a notochord are assumed, regardless of time of origin or number of generations involved, to be more closely related to each other than to those forms which do not possess a notochord. And further, those forms which have the notochord developed in similar degree are considered to be more closely related than those which have it developed in some other degree.

It appears then that while our classification—assuming it to be a true expression of fact—may actually give an indication of the course of evolution, its attempt at expressing degree of relationship is still nothing more than an attempt at expressing degree of difference. Degree of difference and degree of relationship are on this basis synonymous, assuming, of course, that difference is taken to mean actually fundamental difference, such as is determinable by the study of homologies.

But there is another method of approach to this question of relationship.

If we accept the theory of the "continuity of the germ plasm" the soma becomes in a way a secondary development. That which is important is not the house that the germ plasm builds over itself for its own protection but the germ plasm itself. It is the germ plasm alone that constitutes the unbroken stream of life which has come down to us from the very beginning—if there ever was a beginning. The soma, which is discarded with each generation and built up again, can be merely an index to the conditions that exist within the germ plasm. It is only as changes occur within this germ plasm that somatic differentiation—at least differentiation that may be passed from one generation to another—may appear.

Why then, if we are to take the trouble to speculate at all, should we concern ourselves especially with the modifications of the soma except in so far as they are the visible evidence of the make-up of the germ plasm? Theoretically we should define our concept of relationship not in terms of the evanescent and discontinuous soma but in terms of the enduring germ plasm.

If we approach the matter of relationship from this point of view we arrive at results which are somewhat different from those obtained by a consideration merely of the soma. Phylogenetic relationship comes to mean the convergence of the lines of modification of the germ plasm and degree of relationship is to be measured by degree of germinal differentiation.

It may at first glance appear that after all we have come out by the same door wherein we went. Perhaps for practical purposes that is true, but for the moment we are not concerned with such purposes. Theoretically there may at times be a noticeable difference. It might very well be possible for two organisms to be quite similar somatically and yet quite widely separated genetically, or quite different somatically and yet quite closely related genetically.

Morgan (3, p. 46) has remarked,

> That the visible structural differences between groups of individuals is not a safe guide on which to construct a real distinction (between species), is exemplified by numerous cases in which groups may exist side by side that are so closely similar that only an expert can separate them, yet are either infertile when crossed or else leave offspring that are sterile.

And he cites as a specific example the case of two species of *Drosophila*. Here there is evidently a very considerable genetic difference which is expressed in a very slight somatic difference.

Another example of the difference between the genetic approach to the question of relationship and the usual approach may be found in the case of any hybrid. Let us consider the often told story of the Andalusian fowl, which is to be found as a stock example in almost any book on genetics (3, p. 60). These bluish colored fowls do not breed true, but produce white, blue and black offspring. The white individuals bred among themselves will produce white and the black bred among themselves will produce black.

How are we to consider the matter of relationship in such a case? The answer may have no direct bearing upon problems of systematics, but it will serve to emphasize a point.

On the basis of ordinary usage these forms, having been together in a common soma at one point of their history, are related one to another. But genetically it can hardly be said that such is the case. Genetically they happen merely to have resided for a time within the same house. The white fowls are related—that is are genetically continuous with—the original white fowl which entered the cross that produced the Andalusian, and the black fowls are related to the original black fowl. Genetically they are not related to each other at all, except through the germinal line which leads back presumably to the point where the germ plasms of all fowls merge in a common center. It is evident that conclusions as to relationship which are not checked by genetic tests would lead to erroneous results, or at least to results of differing significance.

Let us consider also the effect of mutations upon our idea that our classification, which is based upon degree of difference, is a measure of degree of relationship.

Let us assume that among the offspring of a single pair of organisms there occur a number of mutants. Somatically they have all come from a common source and would be regarded as equally related. But let us suppose that one individual is a mutant in regard to a single character, another in regard to two, another three, another four and so on. These mutations may be of quite different orders, some minute, some very conspicuous, as conspicuous, let us say, as the loss of wings in a fly. Let us assume them to breed true so that a line is established. What are we to say of these lines and their relationships?

If degree of somatic differentiation be regarded as our measure, that form which departs most conspicuously and obviously from the parent stock would be regarded as the most widely separated from it. Genetically, however, it would appear that the form which departs in regard to the largest number of genes that have been modified would be the most remote, although it might actually resemble the parent stock the most closely of all.

There is then very clearly a possible difference between degree of relationship as based upon somatic differentiation and as based upon the genetic concept.

The systematist, relying, as he usually must, upon the former for the greater part of his conclusions, is possibly building his house upon the sands. He may not be able to do otherwise, for there may be no other foundation material available in significant quantities and he will simply have to take his chances that his entire structure will some time be swept away by the rising flood of some other method of thought.

Thus far systematists in general have been but little disturbed by fears of such an inundation. As a geneticist once remarked, "Systematic literature grows precisely as if the genetical discoveries had never been made. . . ." Nor can one whose associations are chiefly with systematists have failed to observe that in general they are more or less inclined not to take the work of the geneticists seriously as far as it may have any bearing upon their own conclusions. They have referred even to "the querulities of geneticists and other experimental biologists towards systematic work." Such an attitude, however, can probably not be successfully maintained for long. Whatever apparent differences there may be must in the end be harmonized. Questions raised by investigations in one field may not indefinitely be ignored by workers in another.

THE REACTION OF THE MUTATION THEORY UPON SYSTEMATICS

The particular question that I am here concerned with arises out of the work that has been done, chiefly during the last twenty-five years, on the subject of mutation and its rôle in evolution. And I am concerned with this only as it reacts upon the philosophy of systematic work.

If we accept the theory that mutation has been the dominant, if not the sole, factor in evolution we must be prepared to accept also certain possibilities that appear to be contained within its scope. We must accept, for one thing, the possibility that in some cases mutations of wide extent have taken place. Just how wide that extent may be we do not know. For one thing, changes of too great an order may possibly result in such profound physiological disturbances in the individual that death results. Such would be the case with certain of the types of monsters that occur among human offspring, so malformed that they can not live, but which, if they could live and find an opportunity to reproduce, might conceivably behave as any other mutant. We can not even surmise, then, what the upper limits may be, for we have no way of knowing just what the physiological effect of a change will be. Who can say just what constitutes a "large change?" We do not know, for example, that the physiological processes involved in the complete loss of wings in a mutant of

Drosophila are necessarily much greater than those involved merely in a shortening of the wing.

Again, assuming that a mutant of what we—in the absence of a knowledge of the extent of physiological change—would call marked degree is able merely to survive it may not leave descendants. As Morgan (3, p. 37) has pointed out, "Many, probably most, of the extreme mutant types could not compete with the native types from which they have sprung..." Consequently, there is probably some actual limit to what mutations may do, from the point of view of possibility of survival alone.

Again, it is evident that there are certain things which mutation at least has not done. In spite of the fact that hexadactyly is not an uncommon occurrence in man at least and apparently has no special survival significance, there does not exist any species of six-toed mammal. In spite of the fact that hundreds of thousands of kinds of insects are known in which there is a great variability of the structure of the tarsus, there is no known insect that has a tarsus of more than five segments, although it would seem that a six-segmented tarsus would be no more of a handicap than one of five segments. Innumerable cases of such limits could be cited. It seems that there are some limits beyond which the changes can not go.

Nevertheless, we must be prepared to accept the possibility that evolution by steps of considerable apparent degree has taken place. If this be true we are confronted by a definite problem having to do with the effect of such possible discontinuity upon the theory of systematic work.

Let us revert to the statement that degree of morphological differentiation is accepted by systematists as the measure of degree of phylogenetic relationship. Let us then assume that we have at hand a series of flies, which on the basis of the sum total of their characteristics appear to be closely related, and that of these flies some are fully winged, some have wings of varying length and one is wingless. Preoccupied with the idea that *degree of difference* is significant the systematist would undoubtedly arrange these flies in a series, beginning with the long winged form and proceeding to the wingless form by way of the series of intermediates. He would almost certainly assume that such is actually a phylogenetic series.

And yet the work of Morgan and others on *Drosophila*, where exactly this situation occurs, does not support any such assumption. Morgan (3, p. 20) speaking of this very matter, and of the appearance of other series of mutations in the cultures of this insect, points out that, "The order in which these mutations occurred bears no relation to their size; each originated independently from the wild type."

This being the case, he proceeds to put the inevitable question.

> Suppose that evolution "in the open" had taken place in the same way by means of discontinuous variation. What value then would the evidence from comparative anatomy have in so far as it is based upon a continuous series of variants of any organ?

He is here considering the matter of the evidence for evolution, but inasmuch as all of our systematic theory is based upon the idea of evolution and our systems of classification are merely attempts to summarize the results of its operation, the systematist may take the question as applying directly to his own efforts. If evolution has indeed taken place in this fashion what validity have our labored attempts to express phylogeny and our belief that degree of morphological differentiation is correlated with degree of phylogenetic relationship?

Here is a question that the philosophically inclined systematist has need to ponder.

It would seem quite clear that if species actually arise by such markedly discontinuous steps as those which have been observed and recorded by the geneticists—and with an entirely unknown upper limit of their possibilities—any thought that degree of somatic differentiation has anything to do with degree of relationship must be abandoned. The systematist, under these conditions, would find himself back in the pre-evolutionary period, where all he could hope to do would be to group organisms together solely on the basis of convenience and without any attempt to express any underlying principles whatsoever.

For if mutations of this order are the basis of the origin of species, that is, are the basis of differentiation, we obviously can not say of a series of species that this is most closely related to that and is more remote from another except on the basis of a genetic analysis which will demonstrate how many factors have been involved in producing the differences. But species are grouped together to compose progressively larger categories, each of which presumably represents something of an evolutionary step. Consequently if we cannot depend at all upon our judgment concerning species, how may we dare to hope that our judgment of the larger groups which are composed of species can be any better?

Our whole body of systematic theory, in fact, is built up on the idea of continuity. If that continuity actually does not exist our body of theory falls apart.

We have, however, a curiously paradoxical situation. At the one end of the series apparently we may not trust the evidence. But if we begin at the other end the matter is different. Probably any biologist, regardless of the school to which he belongs, will admit that the vertebrates are more closely related to each other than to any other kinds of animals, and that regardless of the criteria of relationship that may be adopted. Probably also it will be admitted that the mammals are more closely related to each other than to the other vertebrates. And of the mammals it will certainly be admitted that the primates are more closely related to each other than to other mammals. But if the species of primates have arisen by markedly discontinuous mutations we cannot rely upon conclusions as to their relationships within the group.

Where then do we become wrong as we go down the scale or right as we go up it? If marked discontinuity has been at work it would seem that at some point we must inevitably go astray.

Morgan himself (3, p. 22) has given an answer to his own question that is partially satisfactory. It is this, ". . . . our inference concerning the common descent of two or more species is based on the totality of such resemblances that still remain in large part after each change has taken place." But it seems that this answer can not be wholly satisfactory if evolution has actually taken place by steps of great discontinuity.

There is no reason to assume that such discontinuity must be confined to any one organ or part of the body. Evolution has involved every organ. Now, if in an insect, for example, a single step robs the animal of its wings or alters them profoundly, and another step changes the segmentation of the tarsi, and a third changes the antennae, a fourth the genitalia and so on, we come very quickly to a form that can not by the sum total of its characters or in any other way be related to any other. It seems reasonable to suppose that eventually we should arrive at a condition where all semblance of continuity is lost.

And yet on the whole we do find continuity of a sort. On the whole it is possible to group organisms together so definitely and to determine so clearly the series of steps by which one form may have arisen from another that we have a very strong argument against a belief in such a procedure. It is perfectly true that there are gaps and it is possible that these gaps are an expression of an actual interruption of continuity in evolutionary history. The existence of these gaps has so impressed at least one recent writer (1) that he seems almost to have fallen back upon the idea of special creation as a means of accounting for them.

His statement seems to the present writer curiously inconsistent. He concludes (1, p. 539) "There is not the slightest evidence that any one of the major groups arose from any other. Each is a special animal complex related, more or less closely, to all the rest, and appearing, therefore, as a special and distinct creation." We may pertinently ask at this point, why under such conditions the word *related* should have been used at all.

Yet even this author agrees as to the general picture of continuity. "But within each major group," he goes on to say, "we see a different picture. Here the fossil record shows a constant change from one horizon to another." And of the rise of the reptiles and the mammals, "Here we can trace the gradual development from comparatively insignificant beginnings to a wonderful flowering of specialization and perfection."

Even so, he is still impressed by the amount of discontinuity that can be detected.

> But it is well to emphasize that every evolutionary line has certain gaps; some have these gaps large and broad, while in others (as in the horses) the gaps are relatively small. These gaps probably are largely natural, and not due to a deficiency in the record. They indicate the continuation of the phylogenetic line through variants showing a more or less wide departure from the normal type which happened best to meet the conditions of the time.

It is true that some of the gaps are very impressive. Certainly no one has yet been able to devise a theory of the origin of the vertebrates that is satisfactory to everyone, even the apparently careful and profound work of Gaskell having fared none too well. But it seems hardly time yet to abandon utterly all belief in an orderly and regular mode of origin of these larger groups. We may still legitimately cling to the belief that the gaps are due to other factors. There is still the inadequacy of the paleontological record, there is still the fact that after all our knowledge is really very inadequate. The last factor, I think, is not often given the importance that it deserves. It is a quite tenable hypothesis that where an anomalous condition appears in systematic work and its derivatives the most probable explanation is either that someone has made a mistake or that there remain facts still to be discovered. There is no reason to fall back upon an improbable explanation as long as a probable one is at all available.

It will be difficult to convince the systematist in general that evolution has not been in the main a relatively continuous procedure. Such is the conclusion to which a paleontologist—and a paleontologist is merely a systematist—has come. Osborn (4, p. 40) has expressed the view that "Mutation is an abnormal and irregular mode of origin, which while not infrequently occurring in nature is not essentially an adaptive process; it is, rather, a disturbance of the regular course of speciation." This is one possible answer to the question. That it is a satisfactory answer may be doubted.

However, this is not all of the story. No mutationist, probably, will maintain that all evolution has taken place by changes of the order to which we have called attention. In fact the tendency of their thinking seems to be in the opposite direction, and some of them would probably by among the first to point out that any such conception of mutation as we have been discussing is unutterably crude. Morgan (3, p. 130) remarks,

> . . . . even the smallest changes that add to or subtract from a part in the *smallest measureable degree* [the italics are the present writer's] may also arise by mutation. We identify these smaller mutational changes as the most probable variants that make a theory of evolution possible, both because they do transcend the original types and because they are inherited.

This is a very different picture from that suggested by the question which Morgan propounded and which we have quoted. In fact this concept of mutation brings us for all practical purposes back to the original point from which the systematist has begun his theorizing. There remains nothing but a difference in terminology and even that difference can be disposed of. To make clear the nature of this reconciliation, let us consider the meaning of the word "discontinuous."

THE MEANING OF DISCONTINUITY

If we write the numbers 1–2–3–4–5–6–7–8–9–10 we are prone to speak of this as a continuous series. As a matter of fact it is not. It is merely a regular series, increasing by a fixed increment at each step. Actually, from the point of view of one who might be accustomed to dealing with very small fractions it is highly discontinuous, for there is a very large break between each two members of the series. Again even if we take the series .001–.002–.003 and so on, the mere fact that we have reduced the amounts dealt with does not make the series any the less discontinuous. There is still a break between each two members. So with any fractional series that we may propose. As long as the difference between each two members of the series is measurable the series is discontinuous. The best that can be said of it is that it is regular and orderly.

Now as a matter of fact there can be no such thing as *continuous* variation in organisms. Always between soma and soma there must by the very nature of things be a break. Any measurable difference between successive members of a genetic series constitutes a discontinuity. If that discontinuity be very small and if it be a part of a regular series, especially if that series be cumulative, we would be prone to talk of continuity and it is only in this fashion that we can do so.

Again, if we write the series 1–2–3–4–7–8–10–13–15–16–20, we can not say that this series is either continuous or regular, but we can still detect in it a certain order which leads us to believe that it is a part of a regular progression which has been partially obscured by the presence of gaps.

It would seem that very probably the course of evolution has been something of this sort. Assuming that there actually has been cumulative change—progressive evolution—and I doubt that anyone can successfully argue that there has not, it would probably be something of this type. That is, it seems unreasonable to suppose that if the trunk of the elephant actually arose by cumulative changes those changes were necessarily an inch or five tenths of an inch or three inches at each time. The series may be interrupted, the steps may vary in size, but if we have before us a sufficiently large part of the series we can still trace its course and see something of how we have come from one extremity to the other.

Consequently, if the mutationist is willing to allow the smallest measureable, heritable changes to come within the meaning of the term "mutation" and is willing to accept the view that on the whole small changes and not those of great degree have been the principal factor in evolution, the difficulties largely disappear. Under such conditions a phylogenetic series, while possibly interrupted and irregular, may still retain enough of the evidence to show the general system upon which it has proceeded from one point to another. The accuracy with which such an interrupted series may be interpreted will vary with the extent of the interruptions and irregularities, and there may actually exist series which will not permit of interpretation. Still it would be reasonable to suppose that our hope of expressing phylogeny will not be entirely unjustified.

And if the systematist can not properly expect an absolute continuity, but must be content only with such a degree of apparent continuity as comes within the lower limits that the mutationist is willing to accept, there would seem to be no special room for argument. There may still remain the possibility that in some cases the systematist working purely from a morphological basis may be misled, but the probability of such occurrences would not appear sufficiently great to be generally disturbing. There remains the desirability that the systematist acquaint himself with the geneticist's contributions to biological theory and that wherever possible he test his results by genetical methods. But there would seem to be no fundamental and necessary conflict.

CONCLUSIONS

Certain rather definite conclusions may be drawn from all this as to the bearing of mutational theory upon systematic biology.

1. The possibility must always be recognized that mutations involving a wide departure from the parent stock may take place and that such mutations may have an evolutionary influence.

2. To the extent that such mutations do occur and become perpetuated, the systematist's conclusions that degree of morphological differentiation may be relied upon as a measure of relationship and as an indication of phylogeny would seem to be invalidated.

3. There is on the whole a great deal of evidence against the theory that such mutations have been the principal factor in evolution. The mutationists themselves do not rest their theory upon them. Admitting that they do occur, they will not necessarily lead to such a degree of discontinuity as to affect the sum total of all characters of an organism so greatly that all traces of relationship are lost, although this might possibly be the result.

4. If minute mutational changes be accepted as the most probable basis for evolution, there would seem to be no special conflict between the mutation theory and the demands of the systematist for continuity.

5. This being the case it would seem that in general the mutation theory does not necessarily invalidate in any large degree the basic theories upon which systematists have been accustomed to rely, although it may require of them some modification and it does require the testing of their results by genetical methods wherever possible.

LIST OF LITERATURE

There seems to be but little literature bearing directly upon the problems here considered. It would obviously be impractical to attempt any bibliography of the general literature of evolution, which furnishes the back-ground. Consequently only those papers which have been quoted in the preceding article are here listed.

(1) Clark, A. H. 1928. Animal evolution. Quarterly Review of Biology, 3: 523–541.

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EFFECT OF CLIMATIC FACTORS ON SUCTION FORCE

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I. INTRODUCTION

1. What is suction force?

IT IS a well known phenomenon that the water absorption in the root hair from the soil, or in the mesophyll cell from the vessel, has an intimate relation with the osmotic pressure of the cell sap of these cells. Botanists interested in the absorption phenomenon turned their attention to the study of the osmotic pressure of the cell sap of various tissues of different plants. The ordinary method used is what is generally known as the plasmolytic method. It only gives the value of osmotic pressure of the cell sap at incipient plasmolysis, but not at the normal condition. A second method generally used is Beckmann's method of cryoscopy. It involves the determination of the freezing point of the cell sap. This method is more direct and avoids the objection applicable to the first method. But sap extraction involves great technical difficulties. It may introduce a considerable amount of error. Even if we take for granted that the osmotic pressure determination is of sufficient accuracy, the value so obtained tells us very little about the water absorption power at the condition of determination. For the inflow of water into a cell is determined both by osmotic pressure of the cell sap and also by the effective force available for water absorption or suction is not the same as the osmotic pressure of the cell sap. This point has been made very clear in Ursprung and Blum's (11) first paper on suction force. According to Ursprung and Blum the available force is a resultant of two component forces: on one hand, the osmotic pressure of the cell sap, which causes the inflow of water, and, on the other hand, the tension of the cell wall or the wall pressure, which checks the inflow of water. The effective force available for suction is termed suction force. Shull (5), however, thought that suction tension is a better term. It can be stated in a simple equation.

Suction force = Osmotic pressure − Wall pressure or

$$S = O - W$$

It is interesting to find out how these three factors react on each other under various conditions.

I. The cell is placed in distilled water. Water is absorbed due to suction force. The cell volume increases. The tension of the cell wall or wall pressure increases with the wall expansion. At the same time the osmotic pressure of the cell sap decreases as a result of dilution. Finally the osmotic pressure reaches equilibrium with the wall pressure. The cell is then saturated and no more water can enter the cell. Under such circumstances the suction

II. A plant cell is placed in a very dilute cane sugar solution. Water flows into the cell and volume increases. But the flow stops before the saturation of the cell, when the osmotic pressure of the cell equals the sum of the wall pressure of the cell and the osmotic pressure of the solution surrounding the cell. This can be expressed by the following equation:

$$O = W + o$$

where o indicates the osmotic pressure of the solution surrounding the cell. By substitution in equation I, we obtain $S = o$. In other words, when the volume of a cell remains constant in a solution of cane sugar, the osmotic pressure of the solution is equivalent to the suction force of the cell.

III. A plant cell is placed in a strongly hypertonic solution of cane sugar. Then the water flows out from the cell. The cell volume decreases and the wall pressure diminishes owing to contraction of the cell wall. When the cell reaches a state of incipient plasmolysis, the wall pressure is equal to zero. The wall is subject to no further contraction and the protoplasmic layer is detached from the cell wall. The apparent cell volume is subject to no further decrease.

Here we must make one point clear: that the out flow of water from a cell may also take place in a hypotonic cane sugar solution when the osmotic pressure of the solution is higher than the suction force of the cell.

2. *Method of measuring the suction force of a plant cell*

In 1916 Ursprung and Blum (11) suggested two methods. The first is by measuring the osmotic pressure of the cell sap and the wall pressure. The difference of these two will give suction force. This method involves too many measurements. At the same time great technical difficulties are involved.

The second method is comparatively simple. The principle underlying it is that when the volume of a cell remains constant in a solution of impermeable substance, the osmotic pressure of the solution is equivalent to the suction force of the cell. The details of the method are briefly outlined as follows:

The volume of the cell under investigation is first measured under paraffin oil. Then the paraffin oil is drained and the cell is transferred to a cane sugar solution of known concentration. After thirty minutes the cell volume is measured again to find out its volume change. Several neighboring cells of the same tissue are treated in the same manner but in solutions of different concentration. The volume change of different cells will show a gradation according to the concentration of the immersed solution. In this series, two concentrations will be found, in one of which the volume is slightly increased and in the other slightly decreased. By interpolation, the concentration in which the volume of the cell will remain constant is calculated. From the results of Berkeley, Hartley and Morse the osmotic pressure of the cane sugar solution is found. This method also involves many difficulties in technic, and rapid measurements are impossible. Moreover, this method gives only the measurement of a single cell.

3. *Method of measuring the suction force of plant tissue*

In 1923 Professor Ursprung and Blum (14) suggested another method which is still simpler. In this simple method plant tissue is measured instead of the individual cell. The plant tissue whose suction force is to be measured is immersed immediately in paraffin oil after it is detached from the plant. Then strips of appropriate length are cut from the material under the paraffin oil. Length only is taken and thickness is entirely ignored in measurements. Since the length of the strip is generally thirty or forty times greater than the thickness, the variation in length can be used as a good index for the change in volume. The strip is first measured under the microscope in paraffin oil. The paraffin oil is drained and the strip is transferred to a cane sugar solution of known concentration, at a difference of .05 mol. From the change of the length of different strips the concentration at which the length of the strip remains constant can be interpolated. From the osmotic pressure table the suction force is determined.

4. *The effect of external factors on suction force*

In 1916 Professor Ursprung and Blum (9, 10) made a comparative study on the periodic fluctuation of the osmotic pressure of the plant cell sap and traced the effect of external factors on the osmotic pressure. From our previous discussion it is clear that any change in osmotic pressure in the cell sap will produce a corresponding change in its suction force. Experiments were also performed (8, 12) for the direct determination of the effect of external factors on suction force. However, the most comprehensive work was done by Blum (1, 5, 14) and Molz (3, 4).

Blum drew the following conclusion from his investigation, that all factors affecting the water relation of the plant will affect its suction force. Soil moisture is the most important of all. When the soil is dry the relative humidity of the air also exerts a great influence on suction force. Unfortunately Blum's original article is unavailable to the investigator, and he is not acquainted with the scope of the observation.

Molz obtained about the same conclusion as Blum, but put air humidity on the same rank of importance as soil moisture, especially in causing diurnal fluctuation in suction force. Temperature is said to be important in Winter. Other factors are considered to be of secondary, or of no importance. In studying the work of Molz, and of Prof. Ursprung and Blum, it appears that soil moisture has received adequate treatment, but there is room for further study about the effect of climatic factors.

II. OBJECT OF THIS INVESTIGATION

The subject of the present investigation is three-fold:

1. To study the effect of different climatic factors on suction force.
2. To study and ascertain the relative importance of different factors.
3. To obtain a large number of readings in order to apply statistical analysis.

III. SCOPE OF INVESTIGATION

The present investigation, as stated in the previous paragraph, is limited to the study of the effect of climatic factors on suction force. The work was carried on in Nankai University, Tien-tsin, China. The laboratory work covered two Summer months, July and August, 1927. The above stated period covered the rainy season of North China. At first it was intended to carry this work to the end of October, but on account of other duties it had to be discontinued in September.

In order to obtain a large number of comparable figures, the measurement was concentrated on the leaf of a particular species, *Syringa oblata*. Two neighboring bushes were chosen as experimental material so as to minimize the variation of natural habitat. These two bushes are located on the middle of the south side of a tall building.

IV. METHOD AND PROCEDURE

1. Sampling of material for measurement: In sampling two points should be borne in mind. First, the sampling time must be so arranged that the measurements of the suction force of the leaf are well distributed in various climatic conditions. This will enable us to obtain a good distribution for statistical analysis, which is of primary importance in statistical study. In order to accomplish this, samples were taken at regular intervals throughout the day. The first sample was taken at 5 A.M. and additional samples were taken every two hours until 9 P.M. for the first four weeks and the last two weeks. During the middle two weeks, samples were taken hourly from 8 A.M. to 5 P.M. Before 8 A.M. and after 5 P.M. samples were taken at irregular intervals. The second important point in sampling is to take samples from leaves of approximately the same relative position. The position of leaves sometimes causes great variations in the environment of the leaves. For instance, the environment of a leaf under sunlight is entirely different from that of a leaf in shade. The factor that varies the most is sunlight intensity. Relative humidity also varies. For this reason, our sampling is limited to sun leaves. The environmental factors are by no means comparable in all sun leaves. The exposure and the angle towards the sun may cause great variation. For instance, a leaf standing parallel to the sun rays will not receive the same amount of light as a leaf lying horizontal. In sampling only those leaves lying horizontal or made to lie horizontal are taken.

From one leaf sometimes four to six samples are taken. Molz has shown that the influence of the evaporation of the cut surface extends only over a few millimeters. So in sampling the part about 5 millimeters from the cut edge is discarded.

2. Measurement of suction force: The sample is immediately put into paraffin oil after it is cut from the leaf. The suction force is measured with Ursprung and Blum's simplified method in the laboratory. The measurements are generally made from ½ to 2 hours after sampling.

3. Watering: In order to determine specifically the effect of climatic factors, other disturbing factors must be brought under control. Of these, soil moisture is the most important and also is easy to control. The Syringa bushes are watered thoroughly once a day, about 8–9 A.M., so as to keep the soil moisture always in optimum condition.

4. Observations of climatic factors: Four factors are under observation. They are, air temperature, relative humidity of the air, sunlight intensity, and evaporation. The climatic factors, of course, include also wind and rainfall. But rainfall affects the water relation of the plants only indirectly through the enrichment of soil moisture. In our experiment, the soil moisture is always kept in optimum condition and rainfall will have no influence on the suction force except through its effect on relative humidity. This factor therefor is not included in our study. Wind exerts profound influence on the suction force of the leaf. But our experimental plants are located on the south side of a large building, and therefore are not exposed to strong wind action. Furthermore, during our experimental period there was wind on only two or three days; the readings, on this account, are not sufficient for our present study. This factor has also to be neglected.

Air temperature is recorded from the dry thermometer of a sling psychrometer under shade. Relative humidity is taken with a sling psychrometer.

Sunlight intensity is measured by the difference of evaporation from a black and a white evaporating dish. The areas of the water surface of the two evaporating dishes are adjusted to be the same. The values are reduced to hourly gram basis.

Evaporation is measured by the hourly evaporation of the white evaporating dish. The location of the evaporating dishes is about the same as that of the Syringa plants. They are extended from a southern window of our laboratory.

The time of recording is also very important. In order to obtain good correlation the climatic factors should be recorded simultaneously with the measurements of the suction force. The climatic factors are recorded directly after the sample is taken. The whole process lasts about 10–15 minutes including the sampling.

V. RESULTS

The data compiled are too voluminous for this paper. The daily record is therefore reduced to weekly averages. The weekly average values or the suction force of the Syringa leaves and of the corresponding climatic factors for different hours of the day are tabulated in Table I.

In order to bring out the relation between the different climatic factors on the one side and the suction force on the other, the values from the above data are presented in graphic form in figure 1. The values of the suction force are plotted in pairs with each factor.

From the study of the before mentioned workers and from our own data, the suction force varies inversely with the relative humidity. Generally negative correlation can hardly be shown quantitatively on a graph. For this reason, the reciprocal of relative humidity is plotted

TABLE I

Daily fluctuation of suction force of Syringa leaf and climatic factors

DATE	HOUR	SUCTION FORCE IN ATM.	TEMPERATURE IN DEGREES C.	LIGHT INTENSITY IN G. H.	RELATIVE HUMIDITY IN PER CENT	EVAPORATION IN G. H.
July 13–16	5 A.M.	11.3	21.8		91	
	8	12.7	23.9		81	
	11	13.4	26.4		68	
	2 P.M.	14.5	27.4		67	
	5	13.5	26.6		75	
	8	13.1	24.9		84	
July 18–23	5 A.M.	10.8	23.7		91	.8
	8	12.6	28.0	1.2	79	1.7
	10	15.7	30.1	4.4	72	8.5
	12	15.6	30.7	4.6	68	10.8
	2 P.M.	16.3	30.9	5.6	68	12.9
	4	15.9	31.1	2.8	66	8.0
	6	13.5	30.3	1.8	72	5.1
	9	12.5	28.0		81	2.1
July 25–30	5 A.M.	11.2	24.0		89	1.7
	8	12.8	26.6	1.0	69	3.3
	10	16.0	30.6	4.7	62	11.7
	12	18.1	32.3	6.9	55	18.2
	2 P.M.	19.2	33.0	7.6	52	19.2
	4	18.0	32.3	5.0	56	14.7
	6	13.9	30.9	1.6	62	7.9
	9	13.3	27.9		78	4.1
August 1–6	5 A.M.	10.1	23.4		89	1.1
	8	13.9	27.0	1.6	74	3.2
	10	16.5	29.5	3.9	63	10.7
	12	17.6	31.0	6.3	56	17.4
	2 P.M.	18.2	31.6	7.0	52	19.5
	4	17.0	30.9	5.2	58	14.8
	6	14.0	29.0	1.9	65	8.1
	9	11.4	26.8		76	2.6
August 8–13	5 A.M.	11.2	24.1		88	1.9
	6:30	12.5	25.4		79	1.0
	8	14.6	27.9	2.1	71	3.4
	9	16.1	29.2	4.1	66	9.7
	10	17.3	31.0	5.1	60	13.4
	11	18.2	31.8	7.4	60	15.0
	12	18.0	32.6	6.2	53	14.8
	1 P.M.	18.1	33.1	6.7	52	16.7
	2	17.4	32.6	5.7	52	15.6

TABLE I—*Continued*

DATE	HOUR	SUCTION FORCE IN ATM.	TEMPERATURE IN DEGREES C.	LIGHT INTENSITY IN G. H.	RELATIVE HUMIDITY IN PER CENT	EVAPORATION IN G. H.
August 8–13	3	17.6	32.7	5.3	52	14.3
	4	16.2	31.8	4.3	56	13.3
	5:30	13.7	30.6	1.8	61	7.2
	9	12.5	27.1		73	4.0
August 15–20	5 A.M.	11.2	20.9		92	1.3
	6:30	11.8	21.9		86	0.7
	8	13.9	24.8	1.4	75	1.8
	9	14.8	25.8	2.0	71	5.9
	10	16.2	26.6	4.1	66	8.0
	11	16.5	27.8	5.2	61	10.6
	12	16.3	28.0	5.8	56	13.5
	1 P.M.	17.5	29.0	5.9	54	14.8
	2	17.1	29.3	5.8	52	15.0
	3	16.7	29.6	4.8	52	13.7
	4	15.8	28.7	4.3	56	12.2
	5:30	13.9	27.4	1.8	60	8.0
	9	13.1	24.4		73	2.9
August 22–27	5 A.M.	10.7	20.8		90	
	8	11.7	22.8	1.3	87	1.8
	10	12.9	24.3	2.3	80	6.1
	12	14.8	26.1	4.5	77	8.5
	2 P.M.	15.9	26.8	5.7	73	13.7
	4	14.4	26.5	4.1	73	12.0
	6	14.0	25.3	1.0	75	5.8
August 29–September 3	6 A.M.	12.2	23.2		85	
	8	12.6	24.2	1.5	82	2.9
	10	14.7	26.2	3.1	70	8.5
	12	16.0	27.0	3.3	70	10.2
	2 P.M.	17.1	28.2	4.0	68	13.7
	4	15.4	27.5	3.5	70	10.6
	6	13.2	26.7	.5	75	6.6

instead. By this means, the correlation is converted from negative to positive, and the trend of the two curves can be easily compared.

The graphs present in clear manner the following simple facts. First, the suction force of the Syringa leaf shows a rhythmical diurnal fluctuation. Secondly, this diurnal fluctuation is brought about by the fluctuation of the various climatic factors. Thirdly, all factors seem to exert profound influence on the suction force. The first two findings agree entirely with the results of the previously mentioned workers. The third, however, is not in perfect agreement with their results, especially with regard to light and temperature. We shall analyse the effect of each individual factor separately in the following paragraphs.

TABLE II

Suction force and temperature

SUCTION FORCE IN ATM.	AVERAGE AIR TEMPERATURE IN DEGREES C.	NUMBER OF MEASUREMENTS
8.1–9	21.3	6
9.1–10	22.8	10
10.1–11	24.1	15
11.1–12	24.8	35
12.1–13	24.9	52
13.1–14	27.2	46
14.1–15	28.0	56
15.1–16	29.2	52
16.1–17	29.2	31
17.1–18	29.8	31
18.1–19	30.9	13
19.1–20	31.7	18
20.1–21	33.6	14
21.1–22	33.0	5
22.1–23	33.7	3
23.1–24	37.0	1

1. Temperature and suction force

According to Molz air temperature exerts very little influence on the suction force in Summer. But from our data, the correlation seems quite high. The results are tabulated in Table II.

From the complete data, the correlation coefficient is calculated according to Pearson's formula. The value obtained is .678. From the statistical point of view any correlation higher than .6 indicates good correlation. In other words, air temperature does exert influence on the suction force of the leaf. Here we must

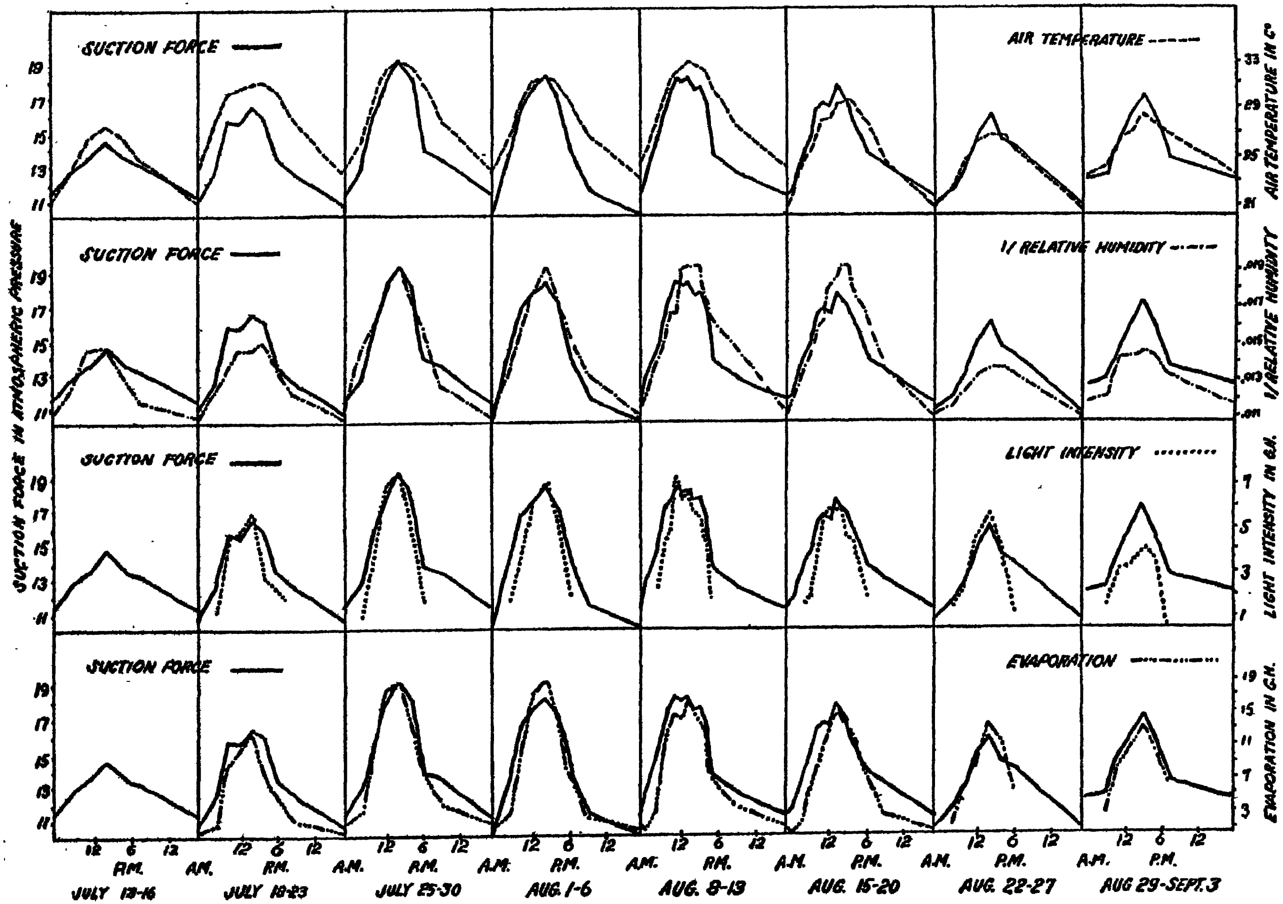

Fig. 1. Daily Fluctuation of the Suction Force and Climatic Factors

not overlook the fact that other climatic factors are operating simultaneously on the suction force. This high correlation may be partially due to the effect of some other factors. This point will be discussed in detail in one of the later sections.

2. *Relative humidity*

That high correlation exists between relative humidity and suction force has been recognized by Blum and Molz. Both of them considered relative humidity as the most important climatic factor in its influence on suction force. The results of the present investigation partially confirm their work. The correlation is especially high when the suction force is between 8.1–22 atmospheric pressures. When the suction force is higher than 22 atm. the correlation is not very pronounced. The data of the present investigation are presented in Table III in condensed form. The calculated correlation coefficient is −.777. It is much higher than that of the temperature. In other words relative humidity exerts greater influence on suction force than air temperature. Blum maintains that relative humidity of the air becomes important only when the soil is dry. During the present experiment the soil moisture content was always kept at optimum condition, yet the correlation coefficient of the relative humidity is very high. Our experimental results indicate that Blum seems to have overemphasized the importance of soil moisture.

TABLE III

Suction force and relative humidity

SUCTION FORCE IN ATM.	AVERAGE RELATIVE HUMIDITY IN PER CENT	NUMBER OF MEASUREMENTS
8.1–9	92.2	6
9.1–10	89.5	10
10.1–11	87.7	15
11.1–12	82.1	35
12.1–13	81.5	52
13.1–14	72.7	46
14.1–15	69.1	56
15.1–16	64.0	52
16.1–17	60.9	31
17.1–18	58.2	31
18.1–19	50.3	13
19.1–20	48.7	18
20.1–21	49.8	14
21.1–22	45.0	5
22.1–23	46.3	3
23.1–24	53.0	1

3. *Light intensity*

Theoretically light intensity should exert profound influence on suction force. It is generally known that the major part of the sun's energy which the leaf receives is consumed in transpiration. The transpiration of the leaf is greatly increased, when the leaf is exposed to light. Brown and Escomb's classical experiment, which has been quoted in most plant physiology texts, indicated that 48.39 per cent of sunlight is consumed in transpiration. The author finds that two cut leaves of Syringa exposed horizontally to the sun's rays will transpire as much as eight grams per hour, while in shade, its transpiration seldom amounts to a gram per hour. This excessive amount of transpiration certainly exerts a strong influence on the suction force of the leaf.

Molz, however, basing on a few laboratory experiments, concluded that light exerts very little or no influence on suction force. Hayoz (3) found an increase in suction force due to the presence of light in two of the three series of experiments which he performed; in the third one he failed to observe any increase. By careful examination of the data, it appears to me that the light intensity employed by these investigators may not be strong enough in comparison with sunlight. In Hayoz's experiment the light intensity reaching the experimental material is only sufficient to heat a black bulb thermometer to 35 degrees C. The black bulb thermometer installed in a box exposed to the sunlight in Tientsin was generally heated to 80–90 degrees C. during noon time. On a few days the temperature recorded by the black bulb thermometer was over 90 degrees C. In Hayoz's experimental condition, the increase recorded as 1.7 atm. It is self-evident, then, that much stronger intensity in sunlight will bring greater increase.

Now let us examine the results of the first series of experiments conducted by Molz. He first exposed the experimental plant material to a radiant energy of 0.000004 cal. cm^2/sec. and obtained an increase of 3 atm.; secondly to a radiant energy of 0.000011 cal. cm^2/sec. and obtained an increase of .8 atm.; thirdly to a radiant energy of 0.0001 cal. cm^2/sec., and obtained an increase of .6 atm. In the first two experiments the results seem to indicate a tendency to proportional increase of suction force with increase of the amount of radiant energy received. But the result of the third experiment fails to indicate that tendency. In comparing the first and the second, the increase in radiant energy is about 2.7 times and the increase in suction force is also 2.7 times. But in comparing the first and the third the increase in radiant energy is 25 times, while the increase in suction force is only two times. But we must understand that we are dealing with a living organ of a plant, the individual variability of which is a great disturbing factor in such relation. We certainly can not expect to find a mathematical relation from three readings. Moreover, unavoidable error in measurements may also introduce a considerable amount of error into such kind of data, since the increase is so small. A difference of .01 mol. in concentration will introduce an error of from .3 to .4 atm. Any investigator acquainted with the present method will realize that error of such magnitude is unavoidable. So non-conformity of results from three experiments is not a surprising fact. At the same time we must realize that an increase of .6 atm. under an exposure of radiant energy of .0001 cal. cm^2/sec. is considerable, when we think that the maximum radiant energy of the sunlight received by a horizontal surface in July and August, according to Kimball (7), is 1.5–1.7 cal. cm^2/min. It is equivalent to .025–.028 cal. cm^2/ sec. or is 250–280 times greater than the radiant energy used in Molz's experiment.

TABLE IV

Suction force and light

SUCTION FORCE IN ATM.	AVERAGE LIGHT INTENSITY IN G. H.	NUMBER OF MEASUREMENTS
9.1–10	0.5	1
10.1–11	1.5	2
11.1–12	1.2	9
12.1–13	1.3	19
13.1–14	2.1	33
14.1–15	3.0	44
15.1–16	4.8	48
16.1–17	4.3	27
17.1–18	5.7	28
18.1–19	5.8	13
19.1–20	6.4	18
20.1–21	7.1	14
21.1–22	7.9	5
22.1–23	8.0	2
23.1–24	6.5	1

In the second series of experiments Molz failed to obtain any possible results showing increase of suction force due to exposure to light. In these experiments he exposed the upper half of the leaf of maize to light or other form of radiant energy and kept the lower half of the leaf in darkness by means of a screen. The exposure varied from 2–16 hours. At the end of the experiment the difference in suction force between the lighted half and the screened half was not determinable. Two explanations can be offered for this fact. The first is that light exerts no influence on suction force. The second is that the suction force of the whole leaf is interrelated. When one part of the leaf is affected, the influence may extend over the whole leaf. Molz apparently was inclined to accept the first explanation, but the author feels that the second interpretation is more plausible, especially with reference to the maize leaf. The leaf of maize is parallel veined. The mesophyll cells bordering the vascular elements in both the upper and the lower half absorb their water from the same source, viz. the water column in the vascular elements. When the suction force of the cells in the upper half of the leaf is raised, the tension of the water column in the vascular elements will increase correspondingly. The increased tension will render absorption by cells in the lower part of the leaf more difficult. The difficulty in absorption in turn will cause a corresponding increase in suction force. Thus an increase of suction force in the upper half due to exposure to light will produce a corresponding increase of suction force in the lower screened half of the leaf. We may therefore feel safe in saying that the result of Molz's second series of experiments is not a conclusive proof of the ineffectiveness of light on suction force.

Our results based on a large number of observations, which amounts to 264, indicated a distinct correlation between the light intensity and the suction force. The results are tabulated in Table IV.

The correlation coefficient of light intensity and suction force is found to be .7, which lies between that of air temperature and that of relative humidity. In other words, the effect of light intensity on suction force is greater than the effect of temperature and less than that of relative humidity.

4. Evaporation

To the author's limited knowledge, the correlation of evaporation and suction force has not been previously studied. Theoretically these two should give a very high correlation coefficient, because the evaporation and the suction force are subject to the influence of the same set of climatic factors. Evaporation represents the summation of the effect of all climatic factors, i.e., air temperature, relative humidity of the air, sunlight intensity, wind, etc. The results of the present investigation, which confirm our speculation, are tabulated in Table V.

TABLE V

Suction force and evaporation

SUCTION FORCE IN ATM.	AVERAGE EVAPORATION IN G. H.	NUMBER OF MEASUREMENTS
8.1–9	1.4	5
9.1–10	2.5	4
10.1–11	2.8	9
11.1–12	2.5	26
12.1–13	3.9	34
13.1–14	7.6	39
14.1–15	11.1	49
15.1–16	17.0	48
16.1–17	16.2	29
17.1–18	20.0	28
18.1–19	21.1	13
19.1–20	23.5	18
20.1–21	25.0	14
21.1–22	29.0	5
22.1–23	30.0	2
23.1–24	25.0	1

The preceding table indicates that the corresponding two factors show very high correlation. The calculated correlation coefficient is .828. Such exceptionally high correlation is within our reasonable expectation. It is interesting to note that the multiple correlation coefficient of the three direct climatic factors is .812, which is still a little less than that of evaporation. This is due to the fact that evaporation represents the effect of all climatic factors; while the latter represents only the effect of three important factors. On account of this exceptionally high correlation coefficient the value of evaporation per hour may be used as the index for the suction force of the leaf with distinct advantage.

5. *The total effect of all climatic factors*

Among all climatic factors, light intensity, air temperature, and relative humidity are constantly operating factors. Other factors are intermittent. For instance, wind came on only two or three days during the whole period of investigation. By the total effect of all climatic factors we mean the total effect of all constantly operating factors. This is known as multiple correlation in statistics. The multiple correlation coefficient is calculated according to Kelly's formula (2). Before calculation, the measurements made when there is no light are parceled out. The calculated multiple correlation coefficient is .812. This indicates exceptionally high correlation. In other words, when the soil moisture is kept in optimum condition, the climatic factors are the determinant factors causing the fluctuation of the suction force.

6. *The actual effect of the individual factors and their relative importance*

The correlation coefficients for each climatic factor found in the previous paragraphs are as follows:

Relative humidity	−.777
Air temperature	.678
Light intensity	.700

However, these figures are not good criteria for comparison, since they represent, not the true effect of those particular factors, but their effect with additional influence from other factors. In order to obtain the true correlation of each individual factor, other disturbing factors should be kept constant. Of course, such a condition can be created only in the laboratory. When a large number of measurements is desired, the work is exceedingly laborious.

However, we may use a mathematical tool, what is known as partial correlation in statistics. By the method of partial correlation, we can isolate the effect of any of the variables. Yule's formula (15) is used for calculation. Before calculation we have to isolate those measurements, which are taken when all constant climatic factors are operating. This means that the measurements taken during the evening and in the early morning are not included in the calculation. The calculated partial correlation coefficients for various climatic factors are tabulated in the following table.

Air temperature	.163
Light intensity	.445
Relative humidity	−.469

From the preceding table it is clear that the influence of the air temperature is very slight. This finding agrees with that of Molz, that air temperature plays a minor rôle in modifying the suction force during the Summer months. It also indicates that relative humidity is the most important; this again agrees with Molz's finding. But in one respect, our results differ from his. According to him the effect of light intensity is of little or no importance as stated before. Our experiment shows very clearly that light exerts a great deal of influence on suction force. The partial correlation coefficient of light intensity, which represents the isolated effect of light on suction force, is as high as .445. Its influence is only a little less than that of relative humidity, whose partial correlation coefficient is −.469.

7. *Variation of relative importance of different climatic factors during different hours of the day*

Now let us examine closely the graphs in figure 1, which represent the weekly average value of the suction force and of various climatic factors. The trend of those graphs seems to indicate that the influence exerted by different climatic factors on the suction force varies with the hours of the day. In order to clarify this point, the measurements taken at different hours of the day are separated into four groups. The first group includes the measurements taken from 6:30 A.M. to 10 A.M.; the second group, from 10 A.M. to 2 P.M.; the third group, from 2 P.M. to 6 P.M.; and the fourth group, from 6 P.M. to 6:30 A.M. of the next day. For each group the partial correlation coefficients of different climatic factors are calculated and tabulated in Table VI.

TABLE VI

Partial correlation coefficient of suction force and climatic factors in different periods of the day

HOURS OF THE DAY	PARTIAL CORRELATION COEFFICIENT		
	Air temperature	Light intensity	Relative humidity
6:30 A.M.–10 A.M.	.195	.345	−.464
10 –2 P.M.	.211	.151	−.564
2 P.M. –6 P.M.	.198	.526	−.253
6 –6:30 A.M.	.229		−.250

From the preceding table we can obtain the following conclusions. In the first place the relative importance of different factors varies with the hours of the day. From 6:30 A.M. to 10 A.M., both relative humidity and light intensity are controlling factors, but relative humidity is slightly more important. From 10 A.M. to 2 P.M. light intensity plays a very insignificant rôle in affecting suction force. Its influence is even less than that of air temperature. During that period relative humidity of the air is the most important factor. From 2 P.M. to 6 P.M. the reverse is true, relative humidity of the air ceases to be important and light intensity becomes the key factor. After 6 P.M. light ceases to exert its influence. The influence of relative humidity remains very low; it is about equal to that of air temperature. Their partial correlation coefficients are only a little above .2, which is considered to be rather insignificant. In other words, the climatic factors exert only a slight influence on suction force in the night time. This is probably due to two causes. In the first place stomata close at night. Secondly the cell sap concentration may undergo internal adjustment due to enzymic reaction (6).

On the whole the influence of air temperature on the suction force is comparatively insignificant and varies within a very narrow range throughout the whole day.

VI. SUMMARY

1. The object of this investigation is to study the effect of climatic factors on the suction force of the leaf of *Syringa oblata*, when the soil moisture is kept in optimum condition. The investigation was performed in July and August, 1927.

2. Among the climatic factors, air temperature, light, and relative humidity are recorded simultaneously with the measurements of the suction force, and rainfall and wind are neglected. The former is neglected because it exerts its influence only indirectly through enrichment of soil moisture, which has been kept constant in the present investigation.

The second is omitted because it is present only on rare occasions.

3. Evaporation is measured simultaneously with other climatic factors, because it represents the combined effect of all climatic factors.

4. In sampling only the leaves which lie horizontal or are made to lie horizontal are taken in order to eliminate the influence of exposure.

5. A large number of measurements were taken in order to be able to use statistical methods to analyse the data. The total number of measurements taken amounts to 388.

6. The suction force of the Syringa leaf shows a rhythmical diurnal fluctuation which is caused by the fluctuation of climatic factors.

7. Our results confirm, in one respect, the results of Blum and Molz, i.e., that the relative humidity is the most influential factor on suction force. Its partial correlation coefficient is −.469.

8. Our results disagree with Molz in regard to the effect of light. We find that light exerts a very profound influence on suction force. Its influence is only a little less than that of relative humidity. Its partial correlation coefficient is .445.

9. Our results are in accordance with that of Molz in regard to the effect of temperature. Its influence on suction force is comparatively insignificant. Its partial correlation coefficient is .165.

10. The total effect of air temperature, light intensity, and relative humidity on suction force of the leaf is represented by a large multiple correlation coefficient which amounts to .812.

11. The correlation coefficient of evaporation and the suction force is .828. It is even higher than the total effect of temperature, light, and relative humidity, because it represents the total effect of all climatic factors, including both constant and intermittent factors.

12. The relative importance of different climatic factors varies with the hours of the day. From 6:30–10 A.M., both light and relative humidity exert strong influence but the latter in a slightly higher degree. From 10 A.M.–2 P.M., relative humidity is the key factor while the influence of light intensity is even less than that of temperature. From 2–6 P.M., light intensity is the key factor, the influence of relative humidity is comparatively insignificant. From 6 P.M.–6:30 A.M., the effect of climatic factors on suction force is much less in degree. The partial correlation coefficients of both air temperature and relative humidity are about .2. Temperature remains an insignificant factor throughout the whole day.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

THE MECHANICS OF TELEOLOGY

Being a review of *Blood. A Study in General Physiology*, by Lawrence J. Henderson. New Haven (Yale University Press) 1928. $5\frac{3}{4}$ x 9; xix + 389. $5.00.

By Joseph Berkson, Institute for Biological Research, Johns Hopkins University

The science of biology, says Henderson, is the record of efforts accurately to describe and clearly to understand living things. The definition wears plausibility and conviction on its face, but a realistic examination of the activities of most operating biological scientists would render it exceedingly dubious. Of descriptive data there is a vast and ever growing output, but contributions to the synthesis of observations under simple and general concepts, which is, broadly, the way by which scientific understanding is achieved, are rare. Far from being acutely conscious that comprehension is the essential part of their professional task, biologists have come to suspect a work characterized by any degree of thoughtfulness; "philosophical" and "metaphysical" applied to scientific endeavor are actually used as terms of opprobrium. Such a condition could not obtain in a community of genuine thinkers, but it is no discovery of ours that scientists are not often thinkers.

The book under review, the author's Silliman Lectures for 1928, somewhat amplified, fulfils to an eminent degree the obligation implied by his own definition of biology. Observations, many of them of great technical refinement, are abundantly presented, but more significantly they are subsumed under an idea which is a distinct and important contribution to the comprehensive understanding of biologic phenomena. Appropriately enough in the light of what we have remarked in our opening paragraph, it has been subjected to an impassioned attack, on the grounds of its metaphysical character, by one of the leading contributors in the very field of investigation covered by the book. Countering this, other equally distinguished scientists have spoken loving and soothing words about it. The series of appreciative comments is to be found in *Science* in the numbers of January 11 and February 8, 1929, and may be recommended for its entertainment as well as instruction.

And now for the book itself, first the factual matter. It deals with the red blood of vertebrates studied as a "physicochemical system and as a tissue." Delimited so, and neglecting an emphasis on multiple factors unique in this author and to be discussed later, it brings together investigations on the blood that have been in progress now for many years. The elucidation of the physiologic rôles played by the ions of sodium, potassium, carbonates, phosphates and chlorides, as well as the chemical character and biologic function of hemoglobin and other blood proteins, the study of equilibrium among these out of and in the body, the solution properties of CO_2 and O_2 in the blood, all form a necessary part of the basis for the work. Names recalled prominently but not exclusively in this connection are Barcroft, Bohr, J. Haldane, Y. Henderson, Krogh, Michaelis, Van Slyke, Warburg, as well as L. J. Henderson. The work in hand comprehends these, not in the character of a compendium of their results, but rather rests on them for a synthesis that is itself novel and creative.

Blood as a physico-chemical system may be considered as made up, to a first degree of approximation, of water, certain bases, hydrochloric, carbonic and other acids, proteins and oxygen. These are disposed among two phases, plasma and cells, in eight components: "(1) Water, H_2O. (2) Carbon dioxide, CO_2. (3) Oxygen, O_2. (4) Hydrochloric acid, HCl. (4a) The sum of all other acids except proteins (that is, excluding carbonic and hydrochloric acids and proteins) which are combined with base, HX. (5) The sum of all the bases (except protein) of the plasma (or serum), BOH_s. (6) The sum of all the bases (except protein) of the cells, BOH_c. (7) The sum of the proteins of plasma (or serum), P_s. (8) The protein of the cells, P_c or, approximately, Hb." The constitution of these under usual normal conditions is constant except for alteration incident to the exchange of CO_2 and O_2 in the lungs and tissues. What happens in the blood when the exchange takes place?

> When carbon dioxide enters or leaves the blood there is a disturbance of equilibrium in both plasma and cells between this substance, the bases, and the other weak acids. If for convenience we neglect the phosphates and other similar compounds included in the component HX and also the ionization of hemoglobin as a base, we may represent the process by the two reversible reactions:
>
> $$H_2CO_3 + BP_s = BHCO_3 + HP_s,$$
> $$H_2CO_3 + BP_c = BHCO_3 + HP_c,$$
>
> and we may say that the absorption of carbonic acid in varying amounts by blood is chiefly due to the transfer of base from proteins to carbonic acid. It must be noted that the above reactions are greatly simplified schemeta, for the proteins are far from being simple monobasic acids.
>
> When the entrance of carbonic acid into the blood, accompanied by these two reactions, takes place, there must evidently be an increase in the concentration of free carbonic acid, of bicarbonate, and of those protein molecules in which certain acid radicals are free, and a decrease of the concentration of protein molecules in which certain acid radicals are ionized as salts. Hence there result two further changes in the system: (1) An increase in the hydrogen ion concentration, and (2) an increase in the total concentration of dissolved substances.
>
> In general these changes of concentration, resulting from the addition of a small quantity of carbonic acid to the system, will be of different magnitudes in cells and in plasma. . . . . A condition of equilibrium in respect of hydrogen ions and of water existed before the addition of carbonic acid, but as a result of the changes following the addition of carbon dioxide unequal changes in the concentrations of these substances must have taken place in cells and in plasma, since increase in bicarbonate is accompanied, under these circumstances, by diminution of hydrogen ion concentration and by increase of osmotic pressure. Thus there must exist a tendency for acid and for water to pass from plasma to cells in order to re-establish the disturbed heterogeneous acid-base equilibrium and the disturbed osmotic equilibrium. In accordance with these considerations, the addition of carbonic acid to blood is, in fact, followed by a movement of water and of hydrochloric acid and other acids into the cells from the plasma.

We see then, that not one thing happens, but many, and in addition each effect becomes a link in a concatenation of events that modifies and is modified by all the rest. This is a simplified statement of only part of the facts and does not touch the changes incident to the entrance of oxygen into the blood, but even so the mind is bewildered in any attempt to grasp them in detail and their totality. Moreover scientifically it suffers from the fatal weakness of not being quantitative. How then to retain the complexity of the whole and at the same time submit it to quantitative treatment is the problem at hand. The mathematical method of equational statement is suggested. Granted that the necessary relations between the physiological variables CO_2 and O_2 and all the other pertinent descriptive variables of the blood, such as pH, cell volume, combined hemoglobin, etc., be known quantitatively, we may express each of the variables separately as a mathematical function of CO_2 and O_2, in an equation. The resulting series of equations, taken together, constitutes a sufficient description of the facts relevant to the equilibrium among the components. For if now the condition of CO_2 and O_2 be known, the condition of any variable is given by one of the equations, and always quantitatively as a certain number of appropriate units. Or, again, if instead of CO_2 and O_2 the condition of two other variables be known (two will always be necessary in the situation under discussion) one may likewise obtain the condition of any third by the simultaneous solution of appropriate equations in the series. Though quite adequate, this equational method of comprehending the facts quantitatively is not the only thinkable one, and Henderson prefers to use another, the nomographic. Since Descartes gave us analytical geometry, it has been possible to represent algebraic relations geometrically, and in an elementary form the nomographic method consists of representing two variables on Cartesian coördinates, and a third as contour lines running across them. If this procedure is followed for all the equations in a complete series representing the equilibrium conditions among the components of the blood we have again, as before, a sufficient description of all the pertinent facts for that sample of blood. The resulting nomograms are necessarily numerous, or if superimposed exceedingly complex and the whole cumbersome. For these reasons the author discards this method for the technique adopted as final, the alignment chart of D'Ocagne. In this, each of the variables descriptive of some condition of the blood, is represented on a line more or less vertically disposed on a chart, and on it are scaled off all the possible values which that variable can assume. The values of any two conditions being given, they are located on the appropriate scales and a straight line drawn through them; the line will of course cross all the other scales and the intersecting points represent the simultaneous values of all the variables. Here we have graphically presented a point already made. On this form of representation a straight line stands for the total constitution of a sample of blood. Since two points determine a line, it becomes strikingly evident that a definite condition of any two variables fixes at once the condition of all the rest. Shifting conditions of the blood traced through the evaluation of two variables may be followed in their totality by way of the shifting position of their correlated lines on the nomogram. Henderson utilizes the nomographic method thus to study the changes occurring in the blood during the respiratory cycle, in rest and work, in health and disease, and in different species. We shall not follow him here, for we wish to conserve the space available to us for the consideration of aspects of his work which are of broader interest.

We have elaborated in considerable detail and at some length the nomographic methodology of the author, as he himself has also done, because it is essential to the presentation of the ideas advanced by him. The concept of the blood as a multiple unity rather than the sum of a number of individual constituent elements is well conveyed in the nomographic representation, and is replete with implication for the objectives to be sought in the scientific investigation of its physiological activity. The unity is conceived as a state of heterogeneous equilibrium expressed as a mathematical function, and here Henderson is influenced importantly by the writings of Willard Gibbs and Vilfredo Pareto. As illustrating the point, in connection with a particular problem, we may quote the search for what it is, in the blood acting on the respiratory center which stimulates breathing. The attempt to allocate it in the pH or CO_2 or some other factor is, if we adopt the view of Henderson as a thorough-going guide, wrongly conceived, an example of what Whitehead has referred to as the "fallacy of misplaced concreteness." Since no single component of the blood changes without a simultaneous alteration of the rest, may it not be that the stimulus of respiration in the circulation is no substance but a certain range in the equilibrium conditions?

A sample of normal blood is a line on the nomogram and the intersections on the scales the necessary concomitant values of the descriptive variables. *The relationship among these is not casual.* Minute examination of them reveals the general truth that they are such as to preserve a constancy in those conditions which make for efficiency in the economy of the organism. "Stability of hydrogen ion concentration is a property of all forms of blood and also of the waters of the earth. In higher organisms this condition is, however, insured by elaborate physiological regulatory processes. Constancy of osmotic pressure of blood is less general, but seems to have been acquired at a relatively early stage of evolution. Constancy of temperature insured by physiological regulation is peculiar to the birds and mammals. It seems probable that temperature and osmotic pressure in the higher vertebrates are approximately optimal conditions for the activities of protoplasm. In the case of the hydrogen ion concentration there can be no doubt that this is so." Henderson makes much of the point, and sees in it a remarkable corroboration of the idea of a constancy in the *milieu intérieur* enunciated by Claude Bernard. "In his opinion (Bernard's), which I can see no reason to dispute, the existence and the constancy of the physico-chemical properties of these fluids is a necessary condition for the evolution of free and independent life. This theory of the constancy of the *milieu intérieur* was an induction from relatively few facts, but the discoveries of the last fifty years and the introduction of physico-chemical methods into physiology have proved that it is well founded." At this point we may give our attention to an objection expressed by J. Haldane against this view of Henderson's (*Science*, April 26, 1929). The physico-chemical system of the blood is not to be considered a physiological *milieu*, he argues, but merely physico-chemical, and it is not an aspect of physiology proper at all. The regulation of constancy which *is* physiological is accomplished by the lungs and kidneys. "In actual fact this constancy depends during health on the coördinated activity of the kidneys and respiratory organs, in accordance with Bernard's principle. . . . . Not all the buffering in the world would keep the reaction constant otherwise, though the buffering greatly smooths the regulation." (*Science*, *ibid.*). The objection of Haldane, it seems to us, is not well taken, and when met serves to illustrate the depth of insight which characterizes Henderson's view. The latter has long insisted on the reciprocal character of adaptation (*The Fitness of the Environment*. New York (The Macmillan Co.), 1913) and following him we may say that no amount of activity on the part of the kidneys and lungs would necessarily secure constancy of reaction, were not the blood so constituted as to be adjusted to these activities. How and why should an objective science differentiate between the parts of such a functioning unity? The physico-chemical constitution of the blood by which its parts are integrated in just such a way as to insure physiological efficiency is not irrelevant to physiology, but as Henderson insists, central to it.

Our comments have deliberately related the contents of the book to the specific business of elucidating the physiological activities of the blood. We would not otherwise faithfully reflect the thoroughgoing experimental character of its major portion. In the opening and closing chapters, however, and interspersed between is contained a contribution toward a philosophy of biologic science which forms in itself a notable document in the history of scientific thought. Henderson has been a watchful observer of the varying modes in the attitude of reason to the nature of the physical world and he knows what it is all about.

> Like all our enterprises the sciences are changeable. They grow and develop. At first descriptive and classificatory, then rational, in this twentieth century some will say that they are destined to become metaphysical. But before they can attain to this last condition it seems probable that they must pass through a stage in which all is clarity, simplicity, and order, where there is no room for philosophic doubt and where, by a singular paradox, the adoption of approximations and philosophically dubious abstractions yields certainty, or at least the closest approach to certainty that man has ever known.

The sly wisdom exhibited in this statement precludes the offering of nicely complete solutions by its author. Aware keenly of the inadequacy of purely mechanistic conceptions for the investigation of biologic problems, but equally conscious of the tremendous value they have had for the progress of science, and at the same time recognizing the intellectual sterility of vitalism, he has in his *Fitness of the Environment* and *Order of Nature* done much to give the dilemmas clarifying analysis. In teleology he sees a concept promising but vague, and has struggled to trace for it a more definite connotation. In assimilating it to mathematical statement and the notions of heterogeneous equilibrium of Willard Gibbs, while offering at the same time for its handling the nomographic technique, he has, it seems to us, made definitive progress in giving it a formulation available for the scientific laboratory. Some of the other expressed thoughts, particularly those associated with the idea of defining life in terms of improbability, appear to us pregnant with the possibility of similar usefulness, and merit a diligent effort at elaboration.

We should not close without the comment that the whole bears relation to the attempt now current among those aristocrats in the world of thought, the speculative philosophers and theoretical physicists, to develop an organic philosophy of nature. Coming from a proletarian of the biological laboratory and couched largely in terms of his own experimental results, it has an exceptional meaningfulness.

BRIEF NOTICES

EVOLUTION

PALAEONTOLOGY AND THE EVOLUTION OF MAN.

By D. M. S. Watson. Oxford University Press
70 cents 5¾ x 9; 27 (paper) *New York*

This is the Romanes lecture of 1928. It is an interesting review of what a conservative paleontologist is able to say at the moment regarding man's evolution. The general conclusion is that "man has indeed arisen from an ancestral ape, differing from the modern forms in his less intense brachiating specializations. Man has undergone his own evolution since that period, and the changes which have occurred in his structure are related to habits entirely different to those of the apes."

GENETICS

VOYAGES OF EXPLORATION TO JUDGE OF THE BEARING OF HYBRIDIZATION UPON EVOLUTION. I. *South-Africa. Genetica Vol. X.*

By J. P. Lotsy and W. A. Goddijn.
Martinus Nijhoff
35 guilders for 2 vols. *The Hague*
Vol. I, 6½ x 9¾; viii + 315
Vol. II, 7¼ x 10; 11 plates

An analysis of biological variation is still the root problem of evolution, as it was when Darwin wrote. Since his time we have come to appreciate, notably through the work of Johannsen, that not all types of diversity seen in nature are of equal significance for the evolutionary process. The senior author of this book has set himself the task of estimating how large a share of the diversity that exists is due to hybridization. Towards this end he explored many parts of the world where observations bearing on the question are available. This report, treating of South Africa, is the first of a number to be issued. With the junior author he observed the results of hybridization in the flora and in man and his general conclusion, given explicitly only for man, is that

> hybrids between different human races and their segregates showed . . . . the great diversity arising from hybridization. Nobody, who looks at the matter in an unprejudiced way, can possibly believe that the different races of mankind in S. Africa or elsewhere have arisen by mutation. A Bushman mutates as little so as to form a Bantu, as a European does or the reverse.

The treatment is descriptive throughout, the examples abundant and detailed. There are a large number of illustrations including a set of beautiful colored plates supplied in a separate packet, and an index, but no bibliography.

SCIENTIFIC PAPERS OF WILLIAM BATESON. *Volumes I and II.*

Edited by R. C. Punnett. The Macmillan Co.
$28.50 per set *New York*
Vol. I, 7 x 10; viii + 452
Vol. II, viii + 503

These two volumes contain, with a few exceptions, all of Bateson's purely scientific papers. The first volume includes his papers on variation, the second those on heredity. Bateson is one of the great figures of modern biology, and his papers are of first rate importance to any student of the history of science. There is an index in each volume and a bibliography in Volume II. In appearance they are up to the high standard of the Cambridge University Press.

REVISED ENCYCLOPEDIA OF CAGED BIRDS. *Canaries, Parrakeets, Finches, Mules and Hybrids. Advice, Suggestions and Information for Pleasure and Profit.*

By Howard Fogg and Nola Miller Fogg.
Audubon Publishing Co.
$1.50 (cloth) 6¾ x 10; 144 *Louisville, Ky.*
.75 (paper)

A revised and enlarged edition in bird culture in which the author, who is managing editor of the *Canary Journal and Bird World*, has brought together in handy form much information concerning the selection and breeding of cage birds; their treatment and feeding when ill as well as in good health; bird diseases; hints on building breeding cages; descriptions of the various breeds; training of the roller canary, etc. There are numerous illustrations, including a number of group pictures of bird fanciers, which have apparently been thrown in for good measure, and an index.

* * *

MATERIALS FOR THE STUDY OF INHERITANCE IN MAN.

By Franz Boas. *Columbia University Press*
$10.00 6 x 9; viii + 540 *New York*

In this volume Prof. Boas puts at the disposal of human biologists all of the original data upon which was based his famous study on *Changes in the Bodily Form of Descendants of Immigrants*. This is a fine service. As he says "a great many questions relating to heredity and environmental influences may be treated by means of this material."

* * *

FACTORS THAT INFLUENCE WOOL PRODUCTION WITH RANGE RAMBOUILLET SHEEP. *United States Department of Agriculture Technical Bulletin No. 85.*

By D. A. Spencer, J. I. Hardy and Mary J. Brandon. *U. S. Government Printing Office*
15 cents *Washington, D. C.*
6 x 9½; 48 (paper)

An investigation of the relations of age, body weight, mutton type, face covering, and skin folds to the amount and quality of fleece in Rambouillet sheep. The results as here presented are chiefly of interest to wool producers; whether more adequate statistical analysis of the original data would yield anything of biological interest we cannot say.

* * *

DIE CYTOLOGISCHEN GRUNDLAGEN DER VERERBUNG. *Handbuch der Vererbungswissenschaft Band I, Lieferung 5.*

By Karl Bělař. *Gebrüder Borntraeger*
80 marks *Berlin*
Subscription price 40 marks
7 x 10½; iv + 412 + 2 plates (paper)

This section of the Baur-Hartmann handbook of genetics is a thorough and detailed review of the cytological basis of heredity. The successive chapters deal with cytomorphology; nuclear and cell division; cell differentiation; fertilization; parthenogenesis; chromosome reduction; individuality of chromosomes; chromosomes and heredity (crossing-over, etc.); cytoplasm and heredity. There is a bibliography of 32 pages. A useful section of a valuable reference work.

* * *

THE CYTOLOGY OF OENOTHERA.

By R. Ruggles Gates. *Martinus Nijhoff*
6¼ x 9⅝; 92 (paper) *The Hague*

This well illustrated review contains a table giving the chromosome numbers in the species and mutants of *Oenothera*, with the authors and dates, up to the end of 1927. There is a lengthy list of references and an index.

GENERAL BIOLOGY

WHAT IS LIFE?

By Augusta Gaskell (Introduction by Karl T. Compton and Raymond Pearl).
Charles C. Thomas
$3.50 $6\frac{1}{4}$ x $9\frac{1}{4}$; 324 *Springfield, Ill.*

From time to time there have been noticed here biological and philosophical works of the paradoxical kind which delighted Augustus De Morgan. If we were to give a bare statement of Mrs. Gaskell's theory, most of our readers would probably place her in that class. But we can assure them that she is no paradoxer; one may not be converted by her argument, but that she is a thoroughly sane person with a keen and logical mind cannot be doubted by anyone who will read the book.

Essentially her theory postulates that under certain conditions protons and electrons combine to form new, intra-atomic units, which, it is assumed, form the essential ingredients of living matter; and that these combine with ordinary elements to form living matter, which is thus a "dual" system. From this starting point, she proceeds to the interpretation of various life phenomena.

The first question, of course, will be as to the possibility of this sort of system. Professor K. T. Compton, in his introduction says:

> The author's answer to the question "What is Life" purports to be based on the facts of modern atomic physics. The first query that will naturally occur to the serious reader is in regard to the author's qualifications in the field of physics. To this I would say that her discussion of modern atomic physics is accurate, well balanced and worth reading for its own sake.
>
> The honest physicist must admit that he knows no independent experimental evidence to suggest or support the hypothesis of these assumed "Z" combinations of protons and electrons. He must also admit that he really knows relatively very little about atoms, protons and electrons, and nothing at all about the explanation of life. Hence the author's fundamental assumption must be admitted as possible. Further, she has shown how it can be used as a working hypothesis in a variety of directions. Finally, it should be susceptible of experimental test. These considerations should support the author in her plea for serious consideration of her work on its merits as a stimulus towards an experimental test of her theory.

We suggest that before dismissing the book as harmless lunacy, it be read; it is quite imaginable that it may suggest some new and valuable ideas.

MORPHOLOGIC VARIATION AND THE RATE OF GROWTH OF BACTERIA.

By Arthur T. Henrici. *Charles C. Thomas*
$3.00 6 x $8\frac{1}{2}$; xiii + 194 *Springfield, Ill.*

This first volume of a new series of Microbiology Monographs, edited by R. E. Buchanan, E. B. Fred and S. A. Waksman, presents the results of a statistical study on the cell changes of bacteria in growing cultures. The author makes no claim to being an expert in biometry but nevertheless even with the application of simple statistical methods he has obtained results of real significance. He shows that

> contrary to the orthodox teaching, the cells of bacteria are constantly changing in size and form and structure; but that instead of these changes occurring in a haphazard or meaningless fashion, or instead of being phases in a rather vague and complex life cycle, they occur with great regularity and are governed by relatively simple laws which, after more data have been accumulated and analysed, may probably be very precisely formulated.

The results indicate that the growth of these organisms is governed by the same laws which govern the growth of multicellular organisms—that there is a period of rapid growth in an early stage of development, a period of slow growth or rest in the mature form, and in the senescent form the period of death.

In the text there are 36 figures and 2 plates. There is an appendix containing 27 tables exhibiting rate of growth of the bacterial cultures, also one containing a list of references. There are also author and subject indices. We congratulate the publisher on having inaugurated this new series of monographs with a volume so auspicious in respect of both scientific content and book manufacturing.

GILBERT WHITE. *Pioneer, Poet, and Stylist.*

By Walter Johnson. *John Murray*
15 shillings net 5½ x 8⅝; xvi + 340 *London*

An account of the life and work of one of the most interesting of English naturalists. Gilbert White was one of those English curates of the eighteenth century—the breed, we hope, is not extinct—whose real interest lay in the world about them rather than in that above them. Throughout his seventy odd years of life he observed nature and his fellows, the world and its inhabitants, as he saw them in his Hampshire village of Selborne. His work has retained its fascination for a century and a half.

The present volume attempts to estimate the value of White's work, both on its scientific and literary sides. The author has, we feel, done some unnecessary apologizing for his hero; some of the accusations which he refutes seem not worth noticing. As for his estimate of White's scientific work, we doubt that all his claims could be fully substantiated. It is easy to pick a sentence from an early writer, and show that this indicates that the author really had the very latest modern discovery in mind, if he had only gone on to work it out. We rather think that it would be easy for an ingenious Jesuit to show by this technique that Saint Thomas Aquinas knew all about natural selection. However, we are quite willing to let the point pass; if this book persuades a few more people to look into *Selborne*, it will have accomplished its purpose.

NEW ESSENTIALS OF BIOLOGY. *Presented in Problems.*

By George W. Hunter. American Book Co.
$1.68 5¼ x 7⅞; x + 453 *New York*

NEW LABORATORY PROBLEMS IN CIVIC BIOLOGY.

By George W. Hunter. *American Book Co.*
96 cents 7½ x 9½; 286 (paper) *New York*

These texts have, we assume, the approval, if not the explicit *imprimatur*, of Dr. Clarence True Wilson, Dr. John Roach Straton, and Bishop James Cannon. At least they should have. They have clearly been written with the statutes of Tennessee and Arkansas in mind, as well as the clip sheet of the Methodist Board of Temperance, Prohibition, and Public Morals. The word "evolution" has been carefully omitted from the index, and we have not found anything in the book which a Baptist Sunday School teacher could not reconcile with Genesis. We are also pleased to note the author's desire to give offense to no one by carefully referring to "the early settlers in Utah" rather than to the Mormons.

As an illustration of the care which has been taken to provide conclusive experimental evidence to substantiate the statements made in the text, we quote from the Laboratory Problems:

> Problem: To Determine the Effect of Alcohol upon Raw White of Egg.
>
> Materials.—White of egg. Alcohol. Test tubes.
>
> Note.—In chemical and physical composition the white of egg is nearly like protoplasm.
>
> Method and Observations.—Pour into a test tube a small amount of raw white of egg. Pour slowly a little alcohol into the tube. What effect does it have on the white of egg? Pour in equal amounts of alcohol and of egg, and mix the two substances by shaking. What is the effect?
>
> Conclusions.—1. How does alcohol affect the white of egg?
>
> 2. Might it have the same effect on living matter?
>
> Note.—The action of alcohol is to take out the water from the white of egg.
>
> Questions.—1. What is an adulteration? Does your pure food law protect you from adulteration of food?
>
> 2. Is alcohol a food? Is it a poison? Can any material be both a food and a poison?

GROWTH.

By William J. Robbins, Samuel Brody, Albert G. Hogan, Clarence M. Jackson and Charles W. Greene. *Yale University Press*
$3.00 6 x 9; xiii + 189 *New Haven*

These are five essays on various aspects of growth by associates of the University of Missouri, as follows: Introduction, by William J. Robbins; An Analysis of the Course of Growth and Senescence, by Samuel Brody; Some Relations between Growth and Nutrition, by Albert G. Hogan; Some Aspects of Form and Growth, by Clarence M. Jackson; Physiological Factors Regulating Normal and Pathological Growth, by Charles W. Greene. For the most part they are brief reviews of the elementary facts relating to the subjects discussed. The article by Brody attempts a profounder analysis, being in essence an attempt to obtain mathematical generalizations that will take in the entire aging process; it is however basically unsound on the mathematical side.

There is a great need for a work which will synthesize comprehensively what is known regarding growth and crystallize the outstanding problems demanding further study. This book is not that work.

THE PRINCIPLES OF SYSTEMATIC ENTOMOLOGY. *Stanford University Publications. University Series. Biological Sciences Vol. 5, No. 3.*

By Gordon F. Ferris.
Stanford University Press
$2.00 (paper) *Stanford University*
$2.75 (cloth)
7 x 10; 169

This critique of systematic entomology is a valuable contribution to biological literature. After an introductory chapter on the contribution of the systematist to biology, there follows a discussion of the principles of systematic entomology, at the conclusion of which are listed eight theses which the writer defends not only as conforming to the theoretical requirements of systematic entomology but also as admitting of an adequate degree of attainment in practice. The remainder of the book is concerned with a comprehensive discussion of these principles and the methods by which they may be applied. Included in the section on "Nomenclature" is a reprint of the International Code. There are a number of illustrations in the text, and an index is appended.

ÉLÉMENTS DE BIOLOGIE GÉNÉRALE.

By Étienne Rabaud. *Félix Alcan*
45 francs 5¾ x 9; xv + 478 (paper) *Paris*

A philosophical (and therefore necessarily wordy) consideration of general biology, which the author describes as follows:

> General biology is therefore neither morphologic nor physiologic; it begins with concrete facts which a precise and certain analysis furnishes it, to end with a knowledge of the relative value and deeper significance of vital phenomena.

The book is well informed, penetrating in its analysis of the methodology of biological science, and makes profitable but, because of the poor print, uncomfortable reading. A table of contents is to be found at the end of the book, but no index.

LA VIE.

By Jean-Paul Bounhiol. Ernest Flammarion
12 francs net 4¾ x 7¼; 330 (paper) *Paris*

An interesting attempt at a synthetic envisagement of all the phenomena of biology from the point of view of energetics. The author is a thorough going mechanist, who believes that the excess of attention which has been paid to morphology has had a retarding effect upon the progress of biological philosophy. He thinks that the essence of life lies in the catalytic oxidation of complex colloids in an aqueous medium. He knows the literature of biology well, and has produced an interesting book, well worth reading even if a bit one-sided.

THE HISTORY OF BIOLOGY.

By Erik Nordenskiöld (Translated from the Swedish by Leonard B. Eyre).
Alfred A. Knopf
$6.00 6¼ x 9½; xi + 629 + xv *New York*

An English translation of this excellent work, the German edition of which was noticed here in Volume I, Number 4. In its present form it has been much improved by the addition of illustrations and by the enlargement of the index. Author, translator, and publisher may well feel satisfaction in the book.

LEHRBUCH DER EXPERIMENTALZOOLOGIE. *2. Auflage. Teil 1 und 2.*

By Bernhard Dürken. Gebrüder Borntraeger
51 marks (paper) 7 x 10¼; xii + 782 *Berlin*
54 marks (cloth)

The second edition, revised and enlarged, of a standard textbook of experimental embryology, in which emphasis is placed upon the correlation and synthesis of the results of genetics and *Entwicklungsmechanik*. There is a bibliography of some 60 pages, and a detailed index.

EINFÜHRUNG IN DIE BIOLOGIE DER SÜSSWASSERSEEN.

By Friedrich Lenz. Julius Springer
12.80 marks (paper) *Berlin*
14 marks(cloth)
6½ x 9½; viii + 221

This treatise on the biology of lakes is a welcome addition to the literature, and well maintains the high standard set in earlier numbers of the series of *Biologische Studienbücher*, of which it is the ninth. The approach is ecological throughout. There is a selected bibliography covering 6 pages, and an index.

METHODIK DES BIOLOGISCHEN UNTERRICHTS. *Ein Hilfsbuch für Lehrer aller Schularten. Teil II: Didaktische Skizzen und Lebensbilder.*

By Karl Smalian. Otto Salle
16 marks (cloth) 6 x 9; xii + 282 *Berlin*
14.50 marks (paper)

A handbook of pedagogical technique

for the teacher of elementary biology and nature study. Its point of view is that of natural history. Anyone who is attempting anything in the way of field work with his students will find this book helpful. It is abundantly illustrated.

◆

LIFE IN INLAND WATERS *with Especial Reference to Animals.*
By Kathleen E. Carpenter. The Macmillan Co.
$4.50 5½ x 8½; xviii + 267 *New York*

A treatise on fresh-water biology, with especial reference to animals, prepared for the use of British students. The standpoint of the work is ecological. The book is fairly well illustrated and has both author and subject indices. At the end of each chapter is a list of references, frequently of considerable length.

◆

DER SAUERSTOFF IM EUTROPHEN UND OLIGOTROPHEN SEE. *Ein Beitrag zur Seetypenlehre.*
By August Thienemann.
E. Schweizerbart'sche Verlagsbuchhandlung
18 marks (paper) 6⅝ x 10; 175 *Stuttgart*
19.50 marks (cloth)

A highly special piece of research and review of the literature on the types of freshwater lakes, with special reference to the oxygen content of the water. It constitutes the fourth volume of a series on limnology, under the general title *Die Binnengewässer.* There is a bibliography covering 3 pages.

◆

DER NATURFREUND AM MEERESSTRANDE. *Eine Einführung in das Verständnis für das Meer.*
By Carl I. Cori. Emil Haim und Co.
Vienna
9 marks 5¼ x 7¾; xi + 174 + 22 plates

This little book aims to serve as an introductory guide for nature classes interested in life forms of the seashore. For a popular book it seems rather heavy, and the poor print and sparsity of illustrations aggravate the impression that it is not well suited to the purpose for which it was intended. There is a list of references and an index.

◆

A BRIEF COURSE IN BIOLOGY.
By Walter H. Wellhouse and George O. Hendrickson. The Macmillan Co.
$1.80 5⅛ x 7¾; xii + 200 *New York*

Designed as a text for a half year introductory course in general biology. It is brief indeed and suffers from didacticism.

◆

DAS LEBEN DER WOLGA. *Zugleich eine Einführung in die Fluss-Biologie.*
By Arvid Behning.
E. Schweizerbart'sche Verlagsbuchhandlung
17.50 marks (paper) *Stuttgart*
19 marks (cloth)
6½ x 9¾; vi + 162

This serves both as an introduction to the general subject of potamobiology and as a specific consideration of biological forms in the Volga River.

HUMAN BIOLOGY

THE SHADOW OF THE WORLD'S FUTURE. *Or the Earth's Population Possibilities and the Consequences of the Present Rate of Increase of the Earth's Inhabitants.*
By Sir George H. Knibbs. Ernest Benn Ltd.
10s. 6d. net 5½ x 8½; 131 *London*

THE BALANCE OF BIRTHS AND DEATHS. *Volume I, Western and Northern Europe.*

By Robert R. Kuczynski. The Macmillan Co.
$2.00 5 x 7⅜; xi + 140 *New York*

About the only point of agreement between the authors of these two books is that they are both viewers-with-alarm. Otherwise they are as completely different as any two books on the population problem could be. One is a careful and detailed study of a particular demographic problem; the other is an emotional outpouring of uplift and bad logic.

Sir George Knibbs, we are bound to say, has disappointed us. We had expected that the first Statistician to the Australian Commonwealth would have given us a reasoned scientific argument. We find, however, very little reason or science in the book. He is greatly disturbed over the tremendous increase in population during the last century; and he thinks something must be done about it. We find some of his reasoning about the rapidity with which we are approaching the saturation point (which he puts at from 5,200 to 11,000 millions) a little dubious; while on the other hand we can hardly assent to some of his arguments for putting the saturation point as high as he does. But the book on almost every page shows that it was written less as science than as propaganda, and that logic was an unimportant consideration when it traversed emotional prejudices. A few quotations will perhaps substantiate this statement.

> The studies of racial characteristics, of the possibilities of beneficient human intercourse, of the problems of miscegenation, of a better personal, communal, national and international hygiene, of eliminating or ameliorating the more terrible diseases and scourges of mankind, of international economics, and of international relations generally, would all become financially possible were war assuredly obsolete.

> When a people, having become subject to a control which has actually destroyed enormous numbers of them, a control which also has plunged them into economic ruin, endeavours by all sorts of subterfuges to spread its political creeds among other peoples, it makes a national goodwill to it fatuous, hinders economic relationships with it, and renders mutual migrations impossible.

> The fact that the uses and applications of capital are not associated with particular persons, nor are they collateral with particular nationality, has also shown that the economic organisation of the world is, at present, very unsatisfactory.

Turning from Sir George Knibbs and his fears, let us say a few words with regard to Kuczynski's study. He has concerned himself with the problem of determining whether the population of Western Europe is really maintaining itself; that is, whether the mothers of the present time are actually reproducing themselves. By a comparison of age-specific fertility and mortality rates he finds that:

> According to the fertility and mortality in Western and Northern Europe in 1926, 100 mothers give birth to 93 future mothers only. With the fertility of 1926 the population is bound to die out unless mortality of potential mothers decreases beyond reasonable expectations. And fertility continued its downward path in 1927.

This problem is, of course, the same that was studied for the United States by Dublin and Lotka. Whether such a conclusion as Kuczynski's or the but slightly more favorable (in the numerical sense) conclusion of Dublin and Lotka, is really cause for great concern is something else again. For our own part, we are inclined to accept it as Margaret Fuller did the universe. But we recommend the book to Sir George Knibbs whenever he is particularly worried about how to feed the 11,000 millions of people who agitate him so.

STUDIES IN THE NATURE OF CHARACTER *by the Character Education Inquiry, Teachers College, Columbia University in Cooperation with The Institute of Social and Religious Research. I. Studies in Deceit. Book One, General Methods and Results. Book Two, Statistical Methods and Results. By Hugh Hartshorne and Mark A. May.*
The Macmillan Co.
$4.50 *New York*
5 x 7¾; xxi + 414 + vii + 306

An investigation of the factors related to dishonest behavior in school children. The results of tests devised to give children an opportunity for cheating without apparent danger of detection are here presented at length. The book is not easy reading, but contains some interesting matter. In particular, the evidence indicates that the influence of the individual teacher is of greater importance than the use of "progressive" or "traditional" methods of instruction—a conclusion which does not surprise us, but which may distress "progressive" educational theorists.

With regard to specific attempts to "build character," some interesting evidence is submitted.

> The organization we shall call system X is a device for interesting school children in the achievement of virtues through practice. When we encountered this scheme, each child was expected to keep a daily record of certain good deeds (among which was truth telling); and, to stimulate him in his effort and so make sure that each virtue was properly practiced, he was rewarded for a good record by being advanced in the organization from rank to rank.

The results of exposure to this influence are not such as to encourage faith in its efficacy. It was found that the longer a pupil was exposed to the system, the more he cheated. And for Sunday schools:

> We may say that neither the length of time that children are associated with Sunday school nor the regularity of their attendance seems to be at all associated with their tendency to deceive either at school or on work taken home.

Again, the effects of another system (which we guess to be one of the Boy Scout organizations) are commented on as follows:

> The numbers on which these three studies of system Y have been based are of course too small to warrant broad generalizations concerning the organization as a whole; and its sponsors, moreover, say that it is not at its best in the communities from which our cases come. We can only conclude that in these places this widely used agency for moral education, whatever its effect may be elsewhere, is either neutral or deleterious with regard to one of its major aims, the teaching of honesty. This conclusion must be at once supplemented, however, for system Y as for system X and the religious schools, by the caution that in other ways it may be having a vast influence for good.

DIGHTON ROCK. *A Study of the Written Rocks of New England.*
By Edmund B. Delabarre. *Walter Neale*
$6.00 6 x 9¼; xv + 369 *New York*

Although the title of this interesting book is "Dighton Rock," the author has included in his discussions other famous rocks in New England where puzzling drawings and inscriptions have been found. Much of the material has already appeared in special articles. Here are presented the more important features of these in a more compact form, with revisions and additions, as the study has progressed.

There are three centers in New England at which aboriginal rock-carving occurred—the most important of these being the region about Narragansett Bay, where it has been found in from fifteen to twenty separate localities. These have been ascribed to many sources, beginning with possible early Phoenician explorers down to Miguel Cortereal, the Portuguese explorer, who lived in this region about 1511. The first inscriptions on Dighton Rock the author believes go back to the intrepid Cortereal, who, wishing to attract the attention of possible explorers, recorded, among other things, that he was the leader of the local Indians. Additions were probably made at a later date by other early settlers, and the Indians soon followed their example with numerous carvings on rocks and stones in the Narragansett and Machias regions, but rarely elsewhere in New England. For the most part there is no evidence to indicate that the Indian carvings had any significance.

By no means the least interesting feature of this book is that it is the outgrowth of research done during vacation periods by one who by profession is a teacher of psychology. The book is well illustrated and contains a lengthy bibliography and an index.

THE GROWTH OF MANUFACTURES 1899 to 1923. *A Study of Indexes of Increase in the Volume of Manufactured Products. Census Monographs VIII.*

By Edmund E. Day and Woodlief Thomas.
U. S. Government Printing Office
$1.35 7 x 10; 205 *Washington, D. C.*

The authors present an analysis in detail and combine their individual results into synthetic estimates of the growth of manufactures in this country over the period 1899 to 1923.

The importance of this sort of work for the study of broad problems in human biology has not been duly recognized. In the discussion of population and eugenic questions that one finds in the current literature, there is blithe disregard of the fact that these matters cannot be intelligently considered except in terms of multiple complex factors. No absolute standards for population are statable, either as regards total numbers or differential qualities. In biometric terms what we require are multivariate equilibrium equations that will give optimal values for one social variable in terms of given values of others. Until considerable progress is made in the development of such equations, the significance of specific changes that are noted in population trends cannot be estimated. As examples of this we may cite the work of Pearl and the study of Pitkin in *The Twilight of the American Mind*, on the import of existing population trends. Both reach conclusions directly opposed to those usually stated, because they take into account industrial and economic changes. It is from this point of view that we regard the sort of data given in the work reviewed as of fundamental importance for human biology.

GEOGRAPHY OF AMERICAN NOTABLES: *A Statistical Study of Birthplaces, Training, Distribution: An Effort to Evaluate Various Environmental Factors. Indiana University Studies Vol. XV, No. 79.*

By Stephen S. Visher. University Bookstore
75 cents 5⅞ x 9; 138 (paper) *Bloomington*

This is a statistical study of the birth places, training and distribution of various sorts of American notables, and an attempt at an evaluation of the various environmental factors. The material was taken from the starred names in Cattell's *American Men of Science*, and from *Who's Who in America*. Among other glimpses of the obvious are these:

> "A region which leads in producing important types of leaders also holds a similar rank in producing other sorts of leaders, and in other significant evidences of merit;" "In the United States there is a southward

> decline among the states in the productions of almost all types of leaders in proportions to populations, and in most other evidences of social merit;" "The rank of an area depends not primarily upon fixed environmental conditions such as climate, topography and soil but upon the character of the predominant population".

The author also finds that cities and towns are more favorable for producing notables than are rural communities; "that a small proportion of men father a large share of notables;" that there is a "close correlation between enthusiasm for research on the part of college professors and output of students who later merit starring," that "for graduate training the leaders here studied have gone largely to a few strong institutions which have on their faculties many notable men;" and that "there is a notable and increasing concentration of the starred scientists in a relatively few institutions situated in a few states." Thirty-one tables and ten figures exhibit the statistical data.

* * *

QUANTITATIVE METHODS IN POLITICS.

By Stuart A. Rice. *Alfred A. Knopf*
$3.00 5⅝ x 8; xxii + 331 *New York*

This book should furnish entertaining reading to the statistically minded. The author has attempted to answer various questions in regard to political behavior by the application of statistical methods. Usually he ends by pointing out that the question is still unsettled. The book, however, indicates that there exists a large field for the statistical treatment of political data, with the possibility of drawing interesting conclusions with regard to human behavior and attitudes.

With regard to the statistical techniques employed, it is to be noted that they are largely devised by the author for the solution of particular problems; and that, while some of them are obviously open to damaging criticism, they are interesting and stimulating to the statistician. They evidently need improvement; but so did the correlation coefficient in the original form in which Galton used it.

But why the attribution to Professor Truman L. Kelley of the Pearsonian frequency curves?

* * *

AINU LIFE AND LORE. *Echoes of a Departing Race.*

By John Batchelor. *Kyobunkwan*
$6.00 post free 6¼ x 9; viii + 448 *Tokyo*

Having lived since 1879 as a missionary among the Ainu, the author has had a remarkable opportunity for observing and recording the customs, language and folklore of this fast disappearing race, which in ancient times probably occupied all of Japan. Reduced now in numbers to about 15,000, and living only in the north, in Hokkaido and Saghalien, they seem to have held closely to their ancient traditions and preserved many of their legends in spite of the fact that adoption of Japanese children has in past ages been one great way of keeping up the numbers of the race. Without it, the author states, the Ainu would have been extinct long ago. This would seem to indicate that very few pure types are now in existence, and probably accounts for some of the diverse types exhibited as Ainu in the photographs of this book. The writer finds much in their language that points to an Aryan ancestry, in both the vocabulary and the grammar. The most striking thing about the men is the very thick and sometimes quite long hair and heavy moustache. One of the niceties of table etiquette is the use of the moustache lifter.

—especially artistic ones being provided for ceremonial occasions.

The book contains numerous illustrations, mostly photographs or reproductions from water-color drawings by Ainu and Japanese artists. There is no index.

AMERICAN MARRIAGE AND FAMILY RELATIONSHIPS.

By Ernest R. Groves and William F. Ogburn.
Henry Holt and Co.
$4.50 $5\frac{1}{2}$ x $8\frac{1}{2}$; xiii + 497 *New York*

This admirable treatise on the institution of marriage as it exists in America today and the resultant behavior of the individuals concerned, will be of interest to students and educators as well as to the general reader. Professor Ogburn contributes a comprehensive statistical study of the subject, which furnishes a sound basis for future work in this line. Upon Professor Groves has devolved the task of gathering the evidence from a study of case histories of happy as well as unhappy marriages, and of evaluating the many tendencies and efforts of those of the present era to depart from the orthodox manner of living which was in vogue when we were young. He does this with a fine sense of judgment. A final section is devoted to a study of correlations, for the benefit of those who wish to study the application of the statistical method to the solution of social problems.

There is a general bibliography on marriage and a special bibliography of the census publications in this field.

A STUDY OF REHABILITATED PERSONS. *A Statistical Analysis of the Rehabilitation of 6,391 Disabled Persons. Bulletin No. 132. Civilian Vocational Rehabilitation Series No. 16.*

Issued by the Federal Board for Vocational Education. U. S. Government Printing Office
10 cents *Washington*
$5\frac{7}{8}$ x $9\frac{1}{8}$; ix + 46 (paper)

Our bilious view of tax-supported activities has often distressed our forward-looking friends. The present pamphlet introduced us to a new device for keeping up our income tax which we had somehow overlooked. It appears that there exists a Federal Board for Vocational Education, which publishes bulletins now numbered up to 132, and whose activities include co-operative spending of money with the states for vocational rehabilitation of disabled persons. This bulletin purports to analyze the results of the work accomplished during the years 1920–1924.

Unfortunately, it is impossible to determine from the report what has been accomplished. If we take the report at its face value, it would appear that the average earnings had increased from less than $10 per week after injury but prior to rehabilitation to more than $20 per week at the time of interview; and that the cost had averaged less than $150 per case. Matters are not as simple as this, however, for we are given no information whatever on which to form an estimate of how much the rehabilitation service had to do with all this. We do not know the nature of the injury in relation to the job held; we do not know the relation of the cost of rehabilitation to the wages before and after rehabilitation; we do not know the true cost of the rehabilitation work (since overhead has been omitted from the figures given); in fact we know nothing of real value in regard to the whole business.

THE AGE OF THE GODS. *A Study in the Origins of Culture in Prehistoric Europe and the Ancient East.*

By Christopher Dawson. Houghton Mifflin Co.
$5.00 5½ x 8⅝; xx + 446 *Boston*

> We are witnessing the rise of a new science which will study man's past, not as an inorganic mass of isolated events, but as the manifestation of the growth and mutual interaction of living cultural wholes. . . . . During the last two centuries the history of Europe has been given an almost exclusively national interpretation. And since the unit is a political one, the method of interpretation has tended to be political also. . . . . Now the alternative to the nationalist conception of history is the cultural or sociological one, which goes behind the political unit and studies that fundamental social unity which we term a culture.

With this *Anschauung* the author traces the history of cultural progress, especially as it has been revealed in the last three decades of archeological and ethnological research. It begins with the glacial age and the paleolithic periods and extends through the iron age in Italy, forming an interesting if somewhat compact synthesis of our knowledge of the development of civilization during this long interval. The book is supplied with a bibliography, chronological tables and an index.

THE ALCOHOL PROBLEM.

By H. M. Vernon. Baillière, Tindall and Cox
9 shillings 5½ x 8½; xv + 252 *London*

The author attempts a survey of the experience of man with the consumption of alcoholic liquors and its control through legislation. He believes some sort of control is necessary but is otherwise disinterested and looks to the securing of a body of knowledge which will permit a wise solution of the problem as it exists in England. The history and effects of prohibition in the various countries where it has been tried are reviewed, as well as the experimental and statistical studies that have been made to determine the vital effects of imbibition. Unfortunately as regards the experience with prohibition the statistics are not brought up to date so that important trends over the last five years are not given. The references provided are limited to works cited; there is an index.

SCIENCE AND GOOD BEHAVIOR.

By H. M. Parshley. The Bobbs-Merrill Co.
$2.50 5¼ x 8; 281 *Indianapolis*

This is a good and a courageous book, but Quixotic. Professor Parshley is much too intelligent a person not to know that the criteria of "good" behavior, as they exist and are accepted in this world as it is here and now constituted and operated, have little indeed to do with such things as science, reason, or even common decency, we regret to say. What he does in this book is to outline his conception of a *rational* system of ethics, based upon present knowledge of general and human biology. The result is interesting and stimulating. Reginald, the office boy, says that Professor Parshley is just another kind of uplifter. But Reginald is young, and therefore harsh. A more constructive criticism, we think, is to suggest that Parshley read and ponder over Pareto's *Traité de Sociologie Générale.*

MYSTERIES OF HISTORY *with accounts of some remarkable characters and charlatans.*

By C. J. S. Thompson. J. B. Lippincott Co.
$4.00 5⅛ x 8½; 319 *Philadelphia*

A well-done piece of literary composition, with a good deal of interest in it for the biologist. Mary Toft, who gave birth to rabbits, or at any rate said she did, was an entertaining person. So also was Franklin's friend James Graham, a high-toned quack whose "Celestial Bed" was a noble idea. At a charge of 450 guineas per night it could be occupied for the purpose of engendering "children of the most perfect beauty." It was *some* bed. This is a book to read along with *Oddities*, noted in this number

LIVELIHOOD IN PEKING. *An Analysis of the Budgets of Sixty Families.*

By L. K. Tao.

Social Research Department, China Foundation for the Promotion of Education and Culture

$3.00 (cloth) *Peking*
$2.00 (sewed)
6½ x 9½; 158 + xxii

An investigation of living expenses among the poorer classes in Peking, based on account-books for 48 families over six months, and 12 elementary school teachers for a month. It is interesting to note that out of 72 employed males in the 48 families, 41 were rickshamen. It appears from the report that this proportion is not unreasonable in a sample of this size and economic status. The report will be of considerable interest to anyone desiring some idea of the living conditions of the poorer classes of Chinese.

RACE AND CIVILIZATION.

By Friedrich Hertz. *The Macmillan Co.*
$7.50 5½ x 8⅝; xii + 328 *New York*

A counterblast to the Nordics. Dr. Hertz makes noble play with Gobineau, Chamberlain, Fischer, Grant, Stoddard, *et al.* Not the least amusing part of the book is that in which he shows how Grant and Stoddard, having borrowed the Nordic dogma from the German race theorists, proceed to show that the Germans are really not Nordic at all. In Dr. Hertz's words "he steals the clothes of German race theorists, alleging that these clothes did not rightfully belong to them."

We recommend the book heartily to anyone who needs a purgative after a dose of Nordicism. We are not prepared to guarantee all the kind words the author has for the inferior races, but he has successfully demolished most of the claims for race superiority. The book badly lacks an index.

IMMIGRATION AND RACE ATTITUDES.

By Emory S. Bogardus. D. C. Heath and Co.
$1.80 5⅛ x 7¾; xi + 268 *Boston*

Here we have another book on the "greatest issue confronting us," this time race relationships. The author strives at scientific objectiveness by employing the answers to questionnaires on race attitudes prepared for the purpose, as the basis of his analysis. Through this medium he discovers the origin of race antipathy, its modes of perpetuation, and how adjustment may be accomplished. The book is apparently designed as a classroom text and contains a list of "projects" and references at the end of each chapter.

IMPRESSIONS OF GREAT NATURALISTS. *Darwin, Wallace, Huxley, Leidy, Cope, Balfour, Roosevelt, and Others.*

By Henry Fairfield Osborn.

Charles Scribner's Sons
$2.50 5¼ x 7½; xi + 294 *New York*

This is a second and revised edition of Professor Osborn's entertaining collection of biographical sketches of great biologists. To the beginning student of any branch of natural history this volume will be an inspiration. To the oldster it is a refreshing reminder of the giants who broke out the main pathways for him. One infers from a somewhat cryptic footnote that Professor Osborn is about to publish a definitive biography of Cope. In the hope that this is a correct inference we await this volume with the keenest interest, for Edward Drinker Cope was, beyond question, the most brilliant biologist that America has ever produced.

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A BIBLIOGRAPHY OF ALASKAN LITERATURE 1724–1924. *Vol. 1. Miscellaneous Publications of the Alaska Agricultural College and Schools of Mines.*

By James Wickersham.
Cordova Daily Times Print
$5.50 *Cordova, Alaska*
5¾ x 9; xxvii + 635

A bibliography of 10,380 titles, which are supposed to constitute "a complete list of the titles of all printed books of history, travels, voyages, newspapers, periodicals, and public documents, in English, Russian, German, French, Spanish, etc., relating to, descriptive of, or published in Russian-America, now called Alaska, from 1724 to and including 1924."

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OFFICIAL VITAL STATISTICS OF SWITZERLAND. *Statistical Handbook Series: No. 12. Publications of the League of Nations. III. Health. 1927. III. 16.*

World Peace Foundation
60 cents 7¼ x 9½; 88 (paper) *Boston*

This report is No. 12 of the *Statistical Handbook Series*, issued by the Health Organization of the League of Nations. The previous issues describe the official vital statistics of the following countries: the Netherlands, Belgium, England and Wales, Spain, Austria, Czechoslovakia, France, Hungary and Italy. These handbooks are extremely useful to the student of human biology, as they give in detail the precise methods of collection and tabulation of vital statistics in the several countries.

* * *

FINANCIAL STATISTICS OF CITIES HAVING A POPULATION OF OVER 30,000. 1926.

By Department of Commerce, Bureau of the Census. U. S. Government Printing Office
$1.25 (buckram) *Washington*
5⅞ x 9¼; 505

A melancholy tabulation showing where the taxpayer gets hit and why. The sad tale shows per capita tax receipts rising from $21.14 in 1903 to $66.14 in 1926. The one encouraging feature shown is an apparent tendency to increase the proportion of payments made from revenue as against that from funded debt.

* * *

L'ART DE CONNAÎTRE LE CARACTÈRE PAR LA PHYSIONOMIE.

By Jean Lefas. *Norbert Maloine*
30 francs 6¼ x 9; 326 (paper) *Paris*

A French treatise on physiognomy. We cannot see that it possesses any advantages for English-speaking readers over the scientific treatises of Dr. Katherine Melvina Huntsinger Blackford.

* * *

STUDIES IN HEREDITARY ABILITY.

By W. T. J. Gun.
George Allen and Unwin, Ltd.
10 s. 6 d. 5⅜ x 8½; 288 *London*

This discussion of the family histories of certain well known British and American families will be of much interest to the general reader who likes to delve into genealogical literature. The serious student of heredity will require a more complete record of data than is here presented, and a more critical analysis of such material.

* * *

THE OPPOSITE SEXES. *A Study of Woman's Natural and Cultural History. By Adolf Heilborn (Translated from the German by J. E. Pryde-Hughes).*
Methuen and Co., Ltd.
6 shillings net *London*
4¾ x 7½; viii + 152

A consideration of the physical structure, psychology, and social position of woman, uncritically written and of slight importance. It does not compare in value with Havelock Ellis's *Man and Woman*.

* * *

WHAT IS EUGENICS?
By Major Leonard Darwin. *Watts and Co.*
1 s. net 4¾ x 7½; viii + 88 *London*

A brief statement, gotten out for the popular Forum Series, of the matters discussed by the author at greater length in his *The Need for Eugenic Reform*, which has been commented on in this Review (Vol. I, No. 4).

ZOOLOGY

VERTEBRATE ZOOLOGY. *An Introduction to the Comparative Anatomy, Embryology, and Evolution of Chordate Animals.*
By G. R. de Beer. *The Macmillan Co.*
$5.50 5½ x 8½; xx + 505 *New York*

In this introduction to the comparative anatomy, embryology, and evolution of chordate animals, the author devotes the first two parts to the study of types. In Part I, *Amphioxus*, *Petromyzon*, *Scyllium*, *Gadus*, *Ceratodus*, *Triton*, *Lacerta*, *Columba*, and *Lepus* are chosen for a study of adult structure; while in Part II, *Amphioxus*, *Rana*, *Gallus* and *Lepus* are used as embryological types. Part III is devoted to a comparative treatment of the various organ systems. This forms the largest section of the book. With the types presented in the first two parts forming a framework, the author introduces in this section other animals, which contribute much that is essential for a logical development of the subject. Part IV is devoted to a discussion of evolutionary morphology. This method of developing the study of the chordate group has much that is commendable. The author has succeeded in discarding many details which are unessential in a general survey and are confusing.

At the end of each chapter there is a brief list of references. There are 185 illustrations within the text, while the volume is completed by a section giving the classification of the animals and groups of animals mentioned, and an index.

Professor Julian Huxley contributes an introduction.

* * *

A CONTRIBUTION TOWARD A MONOGRAPH OF THE ADELGINAE (PHYLLOXERIDAE) OF NORTH AMERICA. *Stanford University Publications, Biological Sciences Vol. VI, No. 1. By P. N. Annand.* *Stanford University Press*
$2.00 (paper) *Stanford University*
$2.75 (cloth)
7 x 10; 146

This work on the Adelginae of the United States is a valuable contribution to the already existing literature on the subject. While laying no claim to completeness, the author nevertheless has succeeded in bringing together a great deal of information about this difficult and confusing group and has arranged it in such a way that the work still remaining to be done, in order to have a complete record of this sub-family, will be apparent to those workers who are especially interested in filling in the gaps. His main object was to "describe and figure all of the known American species in such a way that they can be readily recognized in as many stages as possible." For every species ever reported in America he describes one stage and usually two or three. A chapter on the general morphology and one on the biology of the Adelginae precedes the taxonomic treatment.

There is a bibliography of 161 titles and an index. The work is abundantly and well illustrated.

WILD ANIMAL INTERVIEWS *and Wild Opinions of Us.*

By William T. Hornaday.

Charles Scribner's Sons

$2.50 5¾ x 8; xiv + 310 *New York*

A jolly book, in which much accurate information concerning the natural history of wild animals is scattered amongst a quantity of imaginary argumentation, discussion, and badinage between all kinds of animals and the interviewer. We commend to the attention of the cautious laboratory boys Hornaday's forthright remarks about animal psychology. They are scientifically indefensible, but not therefore necessarily or wholly false.

> Any naturalist who is worth his salt can determine the thoughts and feelings of mammals, birds, and reptiles by the sign language, by facial and bodily expression, and by telepathy; and afterward he can easily translate the whole interview product into outdoor English for the benefit of the reading classes. . . . . Neither the youngsters nor the oldsters of to-day are fully aware of the breadth and depth of the wild animal mind, the wonderful scope of its reasoning, or the high quality of its conclusions.

This book should be very popular with young folks from about eight to twelve years and especially with those who in their earlier years enjoyed the Peter Rabbit Series.

THE BIOLOGY OF SPIDERS.

By Theodore H. Savory. The Macmillan Co.

$5.50 5⅜ x 8½; xx + 376 *New York*

This compendium of material collected from many sources, including also much of the author's original work, is a sound and much needed treatise on the natural history of the arachnids. It contains much that is of interest to the general reader as well. Some idea of its scope is indicated in the chapter headings: The external structure of spiders; the internal structure of spiders; the senses and sense organs; the behaviour of spiders; the quest for food; the spider's web; the spider and its environment; the distribution of spiders; the courtship of spiders; the mating and parenthood of spiders; the development of spiders; fossil and primitive spiders; the trap-door spiders; the evolution of spiders; some other arachnida.

The numerous illustrations are well chosen. There is a lengthy bibliography and an index.

DESTRUCTIVE AND USEFUL INSECTS.

Their Habits and Control.

By C. L. Metcalf and W. P. Flint.

McGraw-Hill Book Co., Inc.

$7.50 5¾ x 9; xii + 918 *New York*

A general textbook of entomology,

developed on an economic base. The first ten chapters deal with general topics, morphology, physiology, classification and control. The remainder of the book is devoted to the discussion of the insects injurious to various crops, domestic animals and man. It is extensively illustrated, but mostly with borrowed figures, and indexed in great detail. It should serve a useful purpose, particularly in agricultural colleges.

COMMON BIRDS OF NORTH CAROLINA GARDENS, FARMS AND ORCHARDS.

Extension Circular No. 170.
By Laurence H. Snyder.
N. C. Agricultural Extension Service
10 cents 6 x 9; 47 (paper) *Raleigh*

This bulletin is presented to meet the demand for a small booklet giving the names and descriptions of common birds of North Carolina. The subject matter is based on observation made over many years in that State. In addition free use has been made of Pearson and Brimley's *Birds of North Carolina*, and various publications of the U. S. Department of Agriculture. The pictures were drawn from actual specimens. The list of birds described includes only 100 of the commonest forms.

A DISTRIBUTIONAL SUMMATION OF THE ORNITHOLOGY OF LOWER CALIFORNIA.

University of California Publications in Zoology, Vol. 32, No. 1.
By Joseph Grinnell.
University of California Press
$3.75 7 x 10¾; 300 (paper) *Berkeley*

This survey was undertaken to find out just what birds exist within the territory of Lower California, together with the outstanding facts as to the local and seasonal occurrences of each of the species and races. Although the task proved to be far more laborious than had been anticipated, the author has succeeded in setting a standard for future work in western ornithology. There is a bibliography of 461 titles and an index to scientific and vernacular names.

LEHRBUCH DER PROTOZOENKUNDE.

Eine Darstellung der Naturgeschichte der Protozoen mit Besonderer Berücksichtigung der Parasitischen und Pathogenen Formen. Fünfte Auflage. II. Teil, Spezielle Naturgeschichte der Protozoen. Erste Hälfte: Mastigophoren und Rhizopoden.
Edited by Franz Doflein and Eduard Reichenow. *Gustav Fischer*
22 marks 6¾ x 10⅛; 426 (paper) *Jena*

The first part of this new edition of the Doflein textbook of protozoology has already been noticed in these columns (III, 586). The present part is the first half of the special portion of the whole work. It deals with Mastigophora and Rhizopoda. It is beautifully printed and illustrated, and constitutes a solid addition to the reference literature of zoology.

DIE TIERWELT DER NORD- UND OSTSEE.

Lieferungen XII und XIII.
Edited by G. Grimpe and E. Wagler.
Akademische Verlagsgesellschaft m.b.H.
Leipzig
Lief. XII, 20.25 marks 6 x 8½; 238 (paper)
Lief. XIII, 13.20 marks 150 (paper)

These two parts of this useful coöperative treatise on the zoology of the North and Baltic seas, of which earlier parts have been noted in these columns, deal with fishery biology (Schnakenbeck); Echinoderma (Mortensen and Lieberkind); Teleostei Physoclisti 7–9 (Duncker and Mohr); zoological and fishery stations (Redeke); Amoebozoa et Reticulosa (Rhumbler); Hydrozoa (Brock).

TESTS OF BLOWFLY BAITS AND REPELLENTS DURING 1926.

U. S. Department of Agriculture Technical Bulletin No. 80.
By D. C. Parman, E. W. Laake, F. C. Bishopp and R. C. Roark.
U. S. Government Printing Office
5 cents 5¾ x 9; 14 (paper) *Washington*

The chief results of this study are the following:

> Beef liver, hog liver, and rabbit meat are all attractive to blowflies and are suitable for bait. The age of the meat, and whether it is in chunks or ground, affect its attractiveness to flies, and apparently chilling also has some influence.
>
> The type of container affects the attractiveness of the bait to flies. A transparent container is more attractive than an opaque one.
>
> The most promising blowfly repellents found as the result of this investigation are pine-tar oil (now being used on an extensive scale by ranchmen), pyrethrum, and certain copper compounds.

AN OUTBREAK OF HOUSE MICE IN KERN COUNTY, CALIFORNIA.

University of California Publications in Zoology, Vol. 30, No. 7.
By E. Raymond Hall.
University of California Press
25 cents 7¼ x 10¾; 14 (paper) *Berkeley*

This paper furnishes an excellent illustration of what unfortunate results man sometimes unwittingly produces when he attempts to reduce the numbers of certain kinds of animals in a particular region. In this instance, under favorable meteorological conditions, when food and shelter were abundant and the principal natural enemies of house mice that normally held their numbers in check had been removed, literally millions of them laid waste a region 18 miles in diameter.

BOTANY

THE FERNS (FILICALES).

Treated Comparatively with a View to Their Natural Classification. Volume III. The Leptosporangiate Ferns.
By F. O. Bower. *Cambridge University Press*
30 shillings net *Cambridge*
7 x 10¼; viii + 306

This is the concluding volume of Professor Bower's work on the phylogeny of the ferns. He here considers the leptosporangiate ferns, having discussed in the first volume the general methods of phyletic study, and in the second volume applied these methods to the study of the primitive ferns, especially the Eusporangiatae.

The author regards his conclusions with proper reserve; in his own words:

> In a sense then this work may be held as opening a fresh period in the Classification of Ferns. It is the sincere hope of the author that it may stimulate further enquiry, suggest the use of still other criteria of comparison, and perhaps lead finally to other conclusions than those here adopted.

His final chapter deals with the evolutionary bearing of his work and will be of interest to biologists generally. He holds that while experiment may give illuminating results, it cannot safely be held to reconstruct evolutionary history, and that comparative morphology, checked by palaeontology, must remain the foundation for phyletic conclusions. As applied to the ferns, we find clear evidence that the main phyla, though distinct at least from early Mesozoic time, have still developed in similar directions. The author holds that the evidence indicates that the so-called fluctuating variations, whose hereditary nature orthodox Mendelians deny, may, if continued without time-limit, become hereditary. Probably no hard-boiled Mendelian will agree, and we confess that his arguments are obviously not conclusive; but for that matter all the other arguments for other theories of evolution that have come to our attention seem to us equally inconclusive, and there you are.

BACTERIOLOGY. *A Text-book of Micro-organisms.*

By Fred W. Tanner. John Wiley and Sons, Inc.
$4.50 5¾ x 9; xvii + 548 *New York*

PRACTICAL BACTERIOLOGY. *An Introduction to Bacteriological Technic.*

By Fred W. Tanner. John Wiley and Sons, Inc.
$2.50 5¾ x 9⅛; xiv + 235 *New York*

This introductory text devotes a generous portion of its space to presenting in summary fashion collateral information in biology, chemistry and physics as well as to practical applications. The style is undistinguished.

The laboratory guide for students who are beginning the study of bacteriology was prepared to accompany the author's own text book but is so arranged that it can be used with other texts.

THE MOTOR MECHANISM OF PLANTS.

By Sir Jagadis Chunder Bose.
Longmans, Green and Co.
$8.40 5½ x 8⅝; xxv + 429 *New York*

This enthusiastic advocate of the identity of the physiological responses of plants and animals has collected in book form all of his results pertaining to the motor mechanism of plants. Many of these have previously appeared in print. There are treated here not only the visible external movements of plants but also the invisible internal movements concerned with propulsion of sap. Single and multiple responses and automatic movements are described and their functional importance in the life of the plant discussed. Throughout the book the motor mechanisms of plants and animals are compared and contrasted. There is nothing in this volume which makes the author's well-known position any more likely to be accepted by plant physiologists than it was before.

DIE HÖHEREN PILZE. *Basidiomycetes. Mit Ausschluss der Brand- und Rostpilze.*

By Gustav Lindau (Third edition, entirely rewritten by Eberhard Ulbrich).
Julius Springer
29.50 marks *Berlin*
5½ x 8⅛; xii + 497 + 14 plates

The third edition of a standard German handbook for the identification of mushrooms. It has been extensively revised from the second edition by Professor Ulbrich. Most of the illustrations have been segregated from the text and printed separately in a pamphlet, which is tucked in a pocket on the inside back cover of the book. A useful book.

WASSERPFLANZEN UND SUMPFGEWÄCHSE IN DEUTSCH-OSTAFRIKA.

By A. Peter. *Weidmannsche Buchhandlung*
20 marks *Berlin*
6½ x 10; 129 + 19 plates (paper)

A taxonomic treatise, with an ecological viewpoint.

MORPHOLOGY

THE FROG. *An Introduction to Anatomy, Histology, and Embryology.*
By A. Milnes Marshall (edited by H. G. Newth). The Macmillan Co.
$2.00 4½ x 7⅛; x + 182 *New York*

Owing to the death in 1926 of Professor F. W. Gamble, who for many years edited this laboratory classic, H. G. Newth, Lecturer in Zoology at the University of Birmingham, has inherited the task of preparing the 12th edition. In general, the book remains the same, except for the sections dealing with microscopical technique, which have been brought up to date, and those dealing with the germ-cells and the early stages of development, which have been largely re-written.

◆

DEGENERATION AND REGENERATION OF THE NERVOUS SYSTEM. *Volumes I and II.*
By S. Ramon y Cajal. Translated and Edited by Raoul M. May. Oxford University Press
$18 for 2 vols. *New York*
6 x 9⅛; xxviii + 769

This treatise by the renowned Nobel laureate of Spain is an exhaustive consideration of what is known concerning the "regressive and progressive processes in the nervous fibres and cells, of traumatic origin, and especially of those due to expansional mutilation." It is a classic work.

◆

ATLAS OF HUMAN ANATOMY. *Vol. I. The Bones, Ligaments, Joints, Regions and Muscles of the Human Body. Vol. II. The Viscera Including the Heart. Vol. III. The Nervous and Blood Vascular Systems and the Sense Organs of the Human Body, with an Appendix on the Lymphatic System.*
By Johannes Sobotta (Edited from the sixth German edition by J. Playfair McMurrich). G. E. Stechert and Co.
$15.00 7⅝ x 9⅝; xxiv + 785 *New York*

Edited and translated from the sixth German edition. It excludes much of the textual matter contained in former editions and conforms more strictly to the title of an anatomical atlas. It continues to vie with Spalteholz for supremacy as the standard reference atlas. The choice between the two is a matter of the toss of a coin.

PHYSIOLOGY AND PATHOLOGY

A HISTORY OF PATHOLOGY.
By Esmond R. Long.
The Williams & Wilkins Co.
$5.00 5 x 7¼; xxiv + 291 *Baltimore*

This general survey of the steps by which the study of pathology has reached its present form was prepared primarily for the author's own students in the University of Chicago, where he is Professor of Pathology. It will be of much interest, however, to all biologists who are interested in following through the development and growth of this phase of their subject.

The idea of humoral pathology in vogue in the time of Hippocrates was upheld by Galen, whose influence extended for a thousand years or so and was in the main supreme down to the renaissance. It was not until the 15th century that the precedent of performing necropsies was established. Fernel, while still holding to the older teachings as regards the pathological effects of humors, temperaments and vital spirits, developed a more rational general pathology than his predecessors. It was

Harvey's great discovery that had a more far reaching effect in pathology than probably any other single discovery. From this time on rapid strides were made.

Modern pathology properly begins with Morgagni, his case histories, numbering several hundreds, being masterly descriptions. With the discovery of the cell, Virchow rebuilt the science of pathology and again it received fresh impetus. New discoveries followed in rapid succession. The last chapters of the book deal with pathological histology, the rise of bacteriology and immunology, and experimental and chemical pathology. The author suggests that future progress in pathology will not be made by individuals so much as by organizations for research to fill in gaps in existing knowledge. There are numerous illustrations that add to the interest of the text. Col. F. H. Garrison of the Army Medical Museum has written a foreword.

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THE FOOD OF JAPAN. *Publications of the League of Nations. III. Health. 1928. III. 2.*

By Egerton C. Grey. World Peace Foundation
$1.25 6¼ x 9½; 161 (paper) *Boston*

Statistical and analytical data to supply information which can be used as a basis for an investigation of the relation of food to the health of the people. The work was undertaken in behalf of the Health Section of the League of Nations and was carried out in the Imperial Institute of Nutrition, Tokyo. The first two chapters deal with the quantity and quality of food in Japan, chapter III with the distribution of food and chapters IV and V with the chemical composition of Japanese foods as consumed, and as purchased. Numerous tables exhibit the statistical and analytical data. There is an appendix giving the Japanese literature relating to the chemical and physical properties of the food of the Japanese, and another containing lists of food materials and the plants and animals serving as sources of food in Japan. These latter lists are in Latin, Japanese and English.

* * *

LECTURES ON PLANT PATHOLOGY AND PHYSIOLOGY IN RELATION TO MAN. *A Series of Lectures Given at the Mayo Foundation and the Universities of Minnesota, Iowa, Wisconsin, the Des Moines Academy of Medicine, Iowa, and Iowa State College, 1926–1927.*

W. B. Saunders Co.
$2.50 5 x 7¾; 207 *Philadelphia*

These are a group of lectures given by different workers at different institutions on topics related to plant diseases and their importance for man, and collected by the Mayo Foundation. They vary in length as well as the emphasis given to points of general or special interest, but for the most part stress the practical importance of the subjects considered. They are: Filterable Viruses, by L. O. Kunkel; Ecology and Human Affairs, by H. C. Cowles; Some Aspects of the Fusarium Problem, by G. H. Coons; Racial Specialization in Plant Disease Fungi, by E. C. Stakman; The Relation of Plant Pathology to Human Affairs, by H. H. Whetzel; and Some Aspects of Cellular Physiology, by W. J. V. Osterhout.

A bibliography is provided with each chapter and there is a general index appended to the book.

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NEUE WEGE ZUR WASSERSTERILISIERUNG (KATADYN).

By Georg A. Krause. J. F. Bergmann
1.20 marks 6 x 9⅛; 20 (paper) *München*

The author claims to have developed a new method by means of which water may be rendered sterile with greater efficiency than attained by any method used hitherto. It is based on the discovery that water which has been in contact with metals such as copper or mercury takes on oligodynamic properties and becomes bactericidal. Silver may be rendered specially effective for the purpose by subjecting it to an inflating process, and it is then called "katadyne" silver. By use of the method the author, according to his experiments, has been exceedingly successful in rendering water sterile of a variety of bacterial forms.

HOMOIOTHERMISM. *The Origin of Warm-Blooded Vertebrates.*
By A. S. Pearse and F. G. Hall.
John Wiley and Sons, Inc.
$2.00 $5\frac{3}{8}$ x $8\frac{5}{8}$; ix + 119 *New York*

> This book is concerned with the physiological and ecological aspects of the evolution of poikilothermic into homoiothermic animals. In it we attempt to discuss evidence for the origin of homoiotherms, temperature regulation, the factors influencing rate of metabolism and growth, and other matters which relate to the adjustments associated with evolution from erratic, more or less intermittent, living to uniform, constant living.

The promise of a fascinating and important study implied in this introductory statement is only partially fulfilled in the body of the book. The whole work is rather brief, and is taken up largely with a review of the elementary facts of metabolism, the specific questions of homoiothermism and poikilothermism being brought in only collaterally. Withal it is an interesting short consideration of the general question of body temperature. There is a bibliography and an index.

SYPHILIS. *Acquired and Heredosyphilis.*
By Charles C. Dennie. *Harper and Bros.*
$2.50 $4\frac{1}{4}$ x $6\frac{3}{4}$; xiii + 304 *New York*

This volume initiates a series of medical monographs the scope and purpose of which are indicated by the editor as follows:

> They will be monographs in the sense that each volume will be devoted to but one subject, but it is not designed that they will be complete in every respect. Rather will they be practical, presenting the essential features of the subject in such form as to make them easily available. They will be written with the needs of the general practitioner particularly in mind by men whose large consulting practices have given them broad contact with the family physician and who are therefore familiar with his requirements.

The book is extreme in its summarization and if useful at all only as a "handbook." At least some of the judgments expressed without supporting evidence are dubious. It contains neither bibliography nor index.

STUDIES ON SCURVY. *Stanford University Publications. Medical Sciences Vol. II, No. 2.*
By Arthur W. Meyer and Lewis M. McCormick. *Stanford University Press*
$2.25 *Stanford University*
7 x 10; 107 (paper)

The first two parts of this monograph are by Arthur W. Meyer and deal with the symptomatology and the gross and minute morphology of experimental scurvy in the guinea pig. The last section, on some characteristics of the blood of the guinea pig in experimental scurvy, is by Lewis M. McCormick. A list of references is appended to each part. There are a number of excellent photographic plates.

LECTURES ON CONDITIONED REFLEXES. *Twenty-five Years of Objective Study of the Higher Nervous Activity (Behaviour) of Animals.*
By Ivan P. Pavlov (Translated from the Russian by W. Horsley Gantt, with the collaboration of G. Volborth, and an Introduction by Walter B. Cannon).
International Publishers
$6.50 6 x 9$\frac{1}{4}$; 414 *New York*

A translation of forty-one papers by Pavlov, dating from 1903 to 1928. There is also a biographical sketch by the translator. For the reader who desires a consecutive account of Pavlov's work, and of the general theory of the conditional reflex, this book will probably be less satisfactory than Pavlov's volume on Conditioned Reflexes reviewed here March, 1928. For the reader who wishes to trace the development of Pavlov's thought, however, the present volume will be invaluable.

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ANNALS OF THE PICKETT-THOMSON RESEARCH LABORATORY. *Vol. IV. Part I. The Pathogenic Streptococci. An Historical Survey of Their Rôle in Human and Animal Disease.*
$10 per volume (Parts I and II)
The Williams & Wilkins Co.
Part I *Baltimore*
8$\frac{1}{2}$ x 11; vii + 250 (paper)

The present volume of these Annals is devoted to a historical survey of researches on the relations of the *Streptococci* to disease; the diseases considered in this part are rheumatic fever, chorea, erythema nodosum, and carditis. The concluding part of this volume is to consider acute suppurative arthritis, chronic arthritis, oral and dental sepsis, and tonsillitis.

* * *

FINAL REPORT OF THE LEAGUE OF NATIONS INTERNATIONAL COMMISSION ON HUMAN TRYPANOSOMIASIS. *Publications of the League of Nations. III. Health. 1927. III. 13.*
World Peace Foundation
$5.00 7$\frac{3}{4}$ x 10; 392 (paper) *Boston*

Contains the following: Report of the new sleeping-sickness focus at Ikoma, by F. K. Kleine; Studies on the bionomics of the polymorphic trypanosomes of man and ruminants, by H. Lyndhurst Duke; Reports, by G. Lavier; Reports, by M. M. Prates; Pathologico-anatomical and serological observations on the trypanosomiases, by M. Peruzzi; Epidemiology of sleeping-sickness in the *G. palpalis* and *T. gambiense* areas and various observations on treatment; General recommendations for the control of sleeping-sickness in African dependencies, by F. K. Kleine, L. Van Hoof and H. Lyndhurst Duke.

* * *

THE RETINAL CIRCULATION *in the Normal and Pathological State.*
By P. Bailliart (Translated by James E. Lebensohn). *The Professional Press, Inc.*
$3.50 5 x 7$\frac{1}{2}$; 220 *Chicago*

A useful little treatise for the medical man who uses the ophthalmoscope daily for diagnostic purposes. The first four chapters describe the anatomy and physiology of the retinal circulation. The next four deal with functional disorders of the circulation. The remainder of the book is devoted to the discussion of lesions of the retinal vessels and their appearance in different diseases. There is no index.

* * *

AN ESSAY ON HASHEESH. *Historical and Experimental. Second Edition.*

By Victor Robinson. *Medical Life Press*
$1.00 5 x 7½; 91 *New York*

A reprint of an entertaining little study of *Cannabis indica*. The author has given a useful account of the preparation and uses of the drug; but the most interesting part of the book to most people will undoubtedly be his account of his experiments with hasheesh, both on his friends and on himself.

THE NORMAL AND PATHOLOGICAL PHYSIOLOGY OF BONE. *Its Problems.*

By R. Leriche and A. Policard. English translation by Sherwood Moore and J. Albert Key. *The C. V. Mosby Co.*
$5.00 6 x 9; 236 *St. Louis*

This is in the nature of a personal memoir giving the opinions of the authors concerning the processes of bone formation and destruction based on a long interest in the subject and extensive study. It is written with a strong physico-chemical bias, not supported in the text with detailed facts. The generalizations indulged in appear to run beyond the evidence given. It is graced by originality and courage, however, and is a stimulating consideration of the basic problems of bone physiology. There is an exhaustive bibliography and an index.

CANCER. *Its Cause and How to Prevent It. With an Epilogue: How to Cure Cancer (A New Theory).*

By Herman J. De Wolff.
Herman J. De Wolff
Rijswijkscheweg 55, The Hague
5½ x 8½; 19 (paper)

The author states in brief paragraphs his belief that cancer is caused by substances with tanning qualities, such as coal-tar products and many chemical substances. There is no attempt at definite proof, neither so far as the cause of cancer is concerned nor for the cure which he suggests. His treatise appears to be a curious jumble of possible truths and quackery.

THE PRESSURE PULSES IN THE CARDIOVASCULAR SYSTEM.

By Carl J. Wiggers. *Longmans, Green and Co.*
$5.00 5¾ x 8¾; xi + 200 *New York*

This volume in the series of Monographs on Physiology measures up fully to the high standard set by the initial editor, the late Ernest Starling. It is a comprehensive and authoritative summary by one of the chief contributors to the subject, of the methods of recording, and the physiological significance of pressure pulses in the cardiovascular system. There is an extensive bibliography and an index.

THE ELEMENTS OF THE SCIENCE OF NUTRITION.

By Graham Lusk. *W. B. Saunders Co.*
$7.00 net 5¾ x 9⅛; 844 *Philadelphia*

This revision, the author threatens, is the last which will be made of his noted text. It brings up to date a statement of all the scientifically established facts that relate to man considered as a fuel consuming machine.

BIOCHEMISTRY

ORGANIC LABORATORY METHODS.

By Professor Lassar-Cohn. Authorized translation from the general part of fifth revised *edition by Ralph E. Oesper. Edited by Roger Adams and Hans T. Clarke.*

The Williams & Wilkins Co.
$6.50 6 x 9; xi + 469 *Baltimore*

This book is a translation of the first volume of the fifth revised German edition. It deals with general operations of laboratory technique such as distillation, crystallization, molecular weight determinations, sublimation, etc. Dr. Lassar-Cohn, who died in 1922, before the fifth edition appeared in print, made no claim for completeness in his work. In such an extensive field, where new methods are so constantly appearing, it would have been impossible to make it all inclusive. Neither did he conceive it to be a text book for beginners. Rather it was "to cite and outline the methods by which typical difficulties have been overcome and leave the adaptation of the suggestions to the problem at hand to the resourcefulness of the reader." This manner of presenting the subject of organic chemistry makes the book a most valuable one to have at hand in the laboratory.

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THE COLLOID CHEMISTRY OF PROTOPLASM.

By L. V. Heilbrunn. *Gebrüder Borntraeger*
19 marks (paper) *Berlin*
21 marks (cloth)
6 x 9; viii + 356

This excellent book, written while the author was a visitor in various European laboratories, critically summarizes recent work in the field of the colloid chemistry of protoplasm. After the introductory chapters, there follow sections on methods of study; the absolute viscosity of protoplasm; the elasticity of protoplasm; the action of temperature, of various salts, of acids and alkalies and of fat solvents upon viscosity; the surface precipitation reaction peculiar to living organisms; cell division; and protoplasmic activity.

* * *

CHEMISTRY IN MEDICINE. *A Co-operative Treatise Intended to Give Examples of Progress Made in Medicine with the Aid of Chemistry.*

Edited by Julius Stieglitz. Advisory Editors: Anton J. Carlson, Reid Hunt, Frank R. Lillie, Lafayette B. Mendel, H. Gideon Wells.

The Chemical Foundation, Inc.
$2.00 5½ x 7½; xxi + 757 *New York*

The Chemical Foundation, through its president, F. P. Garvan, issued this book, without profit, to the public to further an appreciation of the contributions of chemistry to medicine. An able group of contributors has been gathered by the editor to present various aspects of the subject. The following are the general topics discussed: The significance of chemistry and of its methods of attack on fundamental problems; heredity and development; the human body as a machine; the story of the discovery of the vitamins; the conquest of dietary diseases; chemical regulators of the body; the policing of civic life in the laboratory; the alleviation of suffering; the war on invading germs; a hope of mankind—chemotherapy. A glossary of technical terms and an index are appended.

* * *

DIE METHODIK DER FERMENTE. *Lieferungen IV und V.*

Edited by Carl Oppenheimer and Ludwig Pincussen. *Georg Thieme*
28 marks each *Leipzig*
IV: 7⅝ x 10⅝; xxx + 314 (paper)
V: vii + 320 (paper)

The parts of this encyclopedic work on ferments previously issued have been noted in this Review (Vol. III, No. 3;

completes the work and comprises the following:

Part IV, continues Division II, completing subdivision D and presenting E on proteases and F on desmolases.

Part V gives a table of contents for the entire work, continues subdivision F from Part IV, and presents G on fibrin ferments. Division III follows with subdivision A devoted to ferments in biological investigations, and B on clinical applications. A general subject index is appended.

* * *

COLLOID CHEMISTRY. *Theoretical and Applied. Vol. I. Theory and Methods. Vol. II. Biology and Medicine.*

By Selected International Contributors. Collected and Edited by Jerome Alexander.
The Chemical Catalog Co., Inc.
Vol. I, $14.50 *New York*
Vol. II, $15.50
6 x 9; 974 (Vol. I)
1029 (Vol. II)

This extremely useful reference work should be in every biological laboratory. There are over 100 chapters, contributed by nearly as many different authors, on various aspects of the physics and chemistry of colloids. Naturally the treatment is uneven. It is bound to be in such a composite. But the work is a veritable mine of information, and will serve as a reference source. Abundant documentation makes it possible to go deeper into the subject where desirable.

* * *

LE pH EN BIOLOGIE.

By Marcel Verain and Jean Chaumette.
Masson et Cie
16 francs *Paris*
5⅜ x 7¾; viii + 160 (paper)

A short account of the theory and technique of hydrogen ion measurements, with some of the applications of such measurements in medicine, industry, and agriculture.

* * *

DONNÉES NUMÉRIQUES DE BIOLOGIE ET DE PHYSIOLOGIE ET CHIMIE VÉGÉTALES. *Extrait du Vol. VI des Tables Annuelles de Constantes (1923–1924).*

By E. F. Terroine and H. Colin.
Gauthier-Villars et Cie
60 francs (cloth) *Paris*
44 francs (board)
8½ x 10¾; viii + 88

Miscellaneous biological constants taken from determinations published in various journals during 1923–4. It supplements a similar compilation for 1910–1922 which is obtainable in a single volume.

* * *

PRAKTIKUM DER HISTOCHEMIE.

By Gustav Klein. *Julius Springer*
4.50 marks *Berlin*
6½ x 9¾; v + 71 (paper)

An introductory manual on microchemical methods covering inorganic, organic and animal histochemistry. There is a bibliography.

* * *

SEX

MOTHERHOOD IN BONDAGE.

By Margaret Sanger. *Brentano's*
$3.00 5½ x 8; xix + 446 *New York*

A collection of appeals for information on birth control, with harrowing details. They have been somewhat loosely classified, but in general they tell the same story over and over. The letters are rather more persuasive arguments for the dissemination of birth control information than the introductory and concluding passages of the book.

STATUS OF SEX EDUCATION IN THE SENIOR HIGH SCHOOLS OF THE UNITED STATES IN 1927. *A Survey under the Direction of the Surgeon General, United States Public Health Service in Collaboration with the United States Bureau of Education. V. D. Bulletin No. 87.*

By Lida J. Usilton and Newell W. Edson.
U. S. Government Printing Office
5 cents *Washington*
5¾ x 9⅛; iv + 15 (paper)

A report of a survey made in 1927 under the direction of the Surgeon General of the United States Public Health Service, in collaboration with the United States Bureau of Education. The questionnaire method was employed. It is estimated that the percentage of all high schools giving "integrated sex education" was 8 in 1920 and 10 in 1927.

BIOMETRY

THEORY OF PROBABILITY.

By William Burnside. *The Macmillan Co.*
$3.50 5½ x 8⅝; xxx + 106 *New York*

These essays on probability by the late William Burnside were collected into this single volume after his death. They comprise a manuscript which he had almost completed for publication, and are issued without change as the author left them. There is a formal treatment of the elementary notions of probability that brings out again the unsatisfactory basis of the subject from a mathematical viewpoint, and in successive chapters a consideration of some of the classical variety of problems progressively arranged to lead into the Gaussian Law of Errors. A certain amount of obscurity is added to the essential difficulty of the subject by the use of a notation not everywhere explicitly defined.

There is an introductory essay on the life of the author by A. R. Forsythe and appended to the book is a list of cognate papers by him. Considering the small amount of literature in English by original writers on the subject of mathematical probability the publication of this volume by the Cambridge University Press is to be commended.

KORRELATIONSRECHNUNG.

By Franz Baur. *B. G. Teubner*
1.20 marks *Leipzig*
4¾ x 7¼; vi + 57 (paper)

This booklet gives a brief statement of the formulae of elementary probability leading into the correlation coefficient and correlation ratio. The viewpoint is that of A. A. Tschuprow's *Grundbegriffe und Grundprobleme der Korrelationstheorie*, and for adequate treatment that work had best be consulted.

STATISTIK.

By H. Moeller. *Spaeth und Linde*
8.20 marks *Berlin*
6¾ x 10⅛; xiv + 149

An elementary textbook of general statistics, with emphasis rather more heavily laid upon commercial and economic statistics than upon other departments. The brief bibliographies are confined almost exclusively to German literature.

PSYCHOLOGY AND BEHAVIOR

COMMON PRINCIPLES IN PSYCHOLOGY AND PHYSIOLOGY.

By John T. Maccurdy. *The Macmillan Co.*
$6.00 6¼ x 9⅜; xvii + 284 *New York*

This is an important book. It develops concretely Whitehead's purely philosophical idea of "pattern" and carries it to something approaching the bitter logical end in respect of biological matters falling in the general fields of brain physiology and psychology. Unfortunately it is so written as to be rather heavy reading, and on that account will doubtless fail in some degree to get the immediate attention from biologists which it deserves. From the viewpoint of psychology the author's position is in close resemblance at least to that of the adherents to the *Gestalt* theory. From the point of view of biology its chief significance is in its demonstration that an extreme mechanistic position is untenable.

HOWS AND WHYS OF HUMAN BEHAVIOR.

By George A. Dorsey. *Harper and Bros.*
$3.50 5½ x 8; vii + 298 *New York*

Following the publication of *Why We Behave Like Human Beings* the author received something over 12,000 letters about it all. This present book is written for the purpose of answering some of the questions raised in these letters. Like everything that Dr. Dorsey writes it is entertaining, if somehow rather hectic and breathless reading. He is still very much of a Watsonian behaviorist. In fact the whole book is essentially just a continuation and further elaboration of the earlier one. To many academic biologists, perhaps most, the style and philosophy of these books is offensive. But after all perhaps it is better for stenographers and soda fountain clerks to get a little sound knowledge of biology by this route, than for them to get none at all, which is the net contribution of the *Professoren* to their intellectual cravings. As Mr. Coolidge so wisely said, it takes all kinds of people to make a world.

LE TRAUMATISME DE LA NAISSANCE. *Influence de la Vie Pré-Natale sur l'Évolution de la Vie Psychique Individuelle et Collective.*

By Otto Rank. *Payot*
20 francs 5½ x 9; 256 (paper) *Paris*

In recent years both obstetricians and psychiatrists have been paying a good deal of attention to the remote psychological consequences of the biologically difficult journey along a too narrow pathway which every human being is compelled to undertake if and when he enters this vale of tears. In this volume a psychoanalyst says his say about this important matter. It makes interesting reading whether you believe it or not. Who would have thought, for example, that the explanation of homosexuality is, *tout simplement*, that it is merely the result of an aversion to the female genital organs resting upon the rough experience had with them in being born? We recommend this volume to all students of human biology. They will find many ideas of interest in it, even though they are not prepared to go the whole psychoanalytic hog.

PROBLEMS OF INSTINCT AND INTELLIGENCE.

By Major R. W. G. Hingston.
The Macmillan Co.
$3.25 5⅜ x 8; vii + 296 *New York*

An extremely interesting and valuable contribution on the literature of comparative psychology. The author is a distinguished naturalist and presents, in large part, the results of his own observations and experiments on insects in the field; chiefly in the jungles of the Oriental tropics. His final conclusion is that:

> So far as I can judge from the evidence given, we are not justified in making barriers between insect and human mentality. I mean we have no right to regard their minds as being totally different in kind. In their main essential characteristics the minds of these humble creatures operate in the same way as the mind of man.

THE ART OF THINKING.

By Ernest Dimnet. *Simon and Schuster*
$2.50 4⅝ x 7¾; xii + 216 *New York*

This urbane and gossipy essay on the pleasures of the intellectual life furnishes entertaining reading, and the advice it gives is sound. The book is said to have been written for "average minds." Its accuracy of aim is, then, excellent, for it has been for some months a "best seller." The thing which most amuses us in reading it is the thought it conjures up of the heavy weather that earnest thinkers in women's clubs throughout the land are going to have in trying to put the good Abbé Dimnet's precepts into practice. The poor dears will sweat; and, alas, to no purpose, we greatly fear.

THE INFERIORITY FEELING.

By William S. Walsh.
E. P. Dutton and Co., Inc.
$2.50 5 x 7⅜; xi + 381 *New York*

A popular book on the inferiority complex or "feeling" as the author wisely prefers to call it. It is a temperate discussion, with sound advice for the afflicted. It is a book which all parents might well read, because most of our adult mental ills appear to have their foundations laid in early childhood. There is a brief, but well chosen bibliography.

THE FUTURE OF AN ILLUSION.

By Sigmund Freud. Translated by W. D. Robson-Scott.
Horace Liveright and the Institute of Psychoanalysis (Boni and Liveright)
$2.00 5¾ x 8⅞; 98 *New York*

Dr. Freud tells us what religion is and what is to happen to it. So far as the book has any merit, it seems to us to have acquired it by borrowing; those parts whose derivation we do not recognize, and which we accordingly credit to Dr. Freud, seem to us the questionable parts of the argument.

STUDIE ÜBER MINDERWERTIGKEIT VON ORGANEN.

By Alfred Adler. *J. F. Bergmann*
4.20 marks *München*
6½ x 9¾; 92 (paper)

A reissue of Adler's well-known classic on organ inferiority and its psychological consequences, which was first published in 1907 and has long been out of print.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

FROM MAGIC TO SCIENCE. *Essays on the Scientific Twilight.*

By Charles Singer. *Boni and Liveright*
$7.50 6¼ x 9¾; xix + 253 *New York*

In this extraordinarily interesting book, the distinguished author treats of that era in European civilization when there was a slow decline from the intellectual efficiency of classical antiquity down to the lowest stages of decomposition of science, theology, and literature. After lying becalmed in the slough of magic for centuries, observational science slowly and by scarcely perceptible stages reasserted itself. Only the earliest and first steps of this recovery, are treated here. There is little concerning the development of science later than the 12th century, although some of the essays indicate a general line of treatment of the later periods. The main parts of all of these essays have appeared elsewhere in print, but with the exception of the first, they have been considerably modified. In the first chapter there is a discussion of the decay of the conception by the Ionian Greeks of the universe as a rational system. The second essay traces, in barest outline, the entire course of medieval science—and as such is the key to the volume. In the third, "The Lorica of Gildas the Briton" represents the most extreme magical degradation of the classical and ecclesiastical traditions. Science, theology and literature have sunk to their lowest depths. There then follows a chapter on early English magic and medicine—one on early "Herbals" and one on the visions of Hildegard of Bingen. In the final chapter, the medical school of Salerno of the 11th century, the first institution of Western Europe that in any way resembled a university, is described and the influence of Arabian culture traced.

While one can scarcely single out any one chapter as being more interesting than the others, possibly the fifth and sixth—on "The Early Herbals" and "The Vision of Hildegard of Bingen"—will be found the most fascinating by the general reader.

The volume is superbly printed and illustrated.

ODDITIES. *A Book of Unexplained Facts. By Rupert T. Gould. Frederick A. Stokes Co.* $4.00 5½ x 8½; 336 *New York*

This is one of the most entertaining books we have read in many a long day. While it deals with biological matters only in minor part, nevertheless biologists will enjoy reading it. We commend it to all and sundry.

The author is a retired naval officer, and is one of the most extensively, oddly, and casually erudite persons ever heard of. In a passing footnote he says: "Some years ago I read through both *Chambers's Encyclopaedia* and *The Encyclopaedia Britannica.* Truth compels me to state that I greatly prefer the former—not merely because it is shorter, but because, in my opinion, it is planned on far sounder lines, and with a much better sense of proportion."

In *Oddities* Lieut.-Commander Gould discusses some eleven cases of natural or mathematical phenomena, about which the facts are well attested, but for which no rational explanation has ever been found. In some cases he himself reaches what seems a probable explanation, but the others are left as practically complete mysteries.

The first chapter in the book deals with the extraordinary series of tracks found in the snow in Devonshire on February 8, 1855. There can be no question as to the existence and form of the tracks, but what kind of creature made them? The Berbalangs of Cagayan Sulu, Crosse's Acari, and The Wizard of Mauritius also discuss matters of direct biological interest. Regarding the acari all biologists will feel that they know the explanation *in general*, but even so the case presents some matters of detail which suggest interesting and probably profitable lines of research.

In any case, read the book!

BEYOND THE ELECTRON.

By J. J. Thomson. *The Macmillan Co.*
80 cents 5 x 7½; 43 (paper) *New York*

These are trying times for the reasonable mind that sees the universe as a composite of well defined units that will yield understanding to persistent inquiry. Hitherto those who would not accept such clear-cut analysis, and labored the epistemological difficulties of such a view, could be damned with the epithet "philosophers." But nowadays it is the most hard boiled scientists who are introducing a fringe of nebulousness to the ultimate elements of knowledge. Here we find the great physicist of the Cavendish Laboratory saying

> a moving electron, even a uniformly moving one, is always accompanied by a series of waves. These waves as it were carry it along and determine the way it is to go; thus a moving electron is a much more complicated thing than a small point charge of electricity in uniform motion.

What hope is there for a simple view of nature when even the electron turns out complex, and where can we look for the good old mechanical determinism when a particle has to ask a wave, which it creates, how to move? The author takes up his subject as an experimentalist, and pursues it from the viewpoint of classical dynamics but his conclusions harmonize with those arrived at by way of the new wave mechanics of de Broglie and Schrödinger. In view of the alarming fact that the latter seem to imply a measure of uncertainty in mechanical events, this is notable. The forces of teleology are closing in on us.

THE NATURE OF THE PHYSICAL WORLD.

By A. S. Eddington. *The Macmillan Co.*
$3.75 5¾ x 8½; xvii + 361 *New York*

A brilliant exposition, in popular and witty language, of the revelations of relativity theory and modern atomic physics and their meaning for the problem of securing certain knowledge of the external world. Dr. Eddington comes out for the inadequacy of the scientific method and the sovereignty of the mystical insight into truth. His case against the perfection of science carries conviction but his espousal of mysticism does not. In science, however limited, there are objective criteria for distinguishing truth from illusion, but there is no arguing the case of the mystic. It either appeals to you or it doesn't. *De gustibus*, etc.

COSMOS LIMITED.

By Mary Keyt Isham. *Walter Neale*
$2.00 5¼ x 7¾; 125 *New York*

We take it that the author's justification for this book is contained in the following sentence:

> Imagination can never be wild enough to outrun the truth; and every behavior of every individual,—and not the least his imagination,—is impressed upon the mobile, ambient cosmos and makes its contributions to reality.

A general notion of the character of the book can be had from a few quotations.

> Time is the sensing of registration upon cell tissue of its environmental conditions. It is an old touch sense, which, as now experienced by the ear, a highly specialized organ, is the sound sense. All the cells realize impact, which is an incipient hearing and produces a pulsing cellular sensation, a general consciousness of passing time. Marking the passing of the organism through solar radiants, the time sense is occupied in light.
>
> Every cell of the body is an organized assemblage of sunpoints. When points enter the organism in various ways,—as through the respiratory tracts, the alimentary canal, the sense organs,—they become

organic cumulants. Feeling is the motion of an organic cumulant in the act of changing its condition. The abstract conception of a changing group of related points gives us the idea of a *unit of feeling*.

Space is lacking for all the passages of interest, but we cannot omit the following:

> We can not escape the aesthetic demand of life. In time the mind will find a way to eliminate those disgusting bodily products, such as certain excreta which are of disagreeable odor and consistency and cause any amount of inconvenience in regard to proper care, plumbing, cleaning, and laundering. Disgust is a sign of disapproval, and when the mind appreciates its own powers, it will of its own volition finally eliminate what displeases it. This will take an indefinite number of centuries; but when it has been accomplished, solicitations and discontents on a higher plane will arise. The progressive mentality continually pushes its conflicts and urges to higher planes. The secretions and excretions will lose their present undesirable qualities, when by the proper personal selection of nutriment and by exquisitely functioning organs, food will be so readily assimilated, that waste products can be eliminated as easily as is the perspiration. But even then persons will be anxious for fear their bodies may not send forth a natural fragrance which is their favorite one. Each individual will wish to cultivate that aroma or mixture of aromas most pleasing to him. And since the body is capable of producing all the fragrances desired, the glands will be trained as personal gardens.

Even Reginald, the Office Boy, young and uninhibited as he is, cannot think of anything fitting to say about this last quotation, which is at the same time printable in a family magazine like this.

THE BON VIVANT'S COMPANION *or How to Mix Drinks.*

By Jerry Thomas (Edited, with an Introduction, by Herbert Asbury). Alfred A. Knopf
$3.00 5¾ x 8⅝; li + 169 *New York*

The reason for publishing this book is thus stated by Mr. Asbury:

> This volume, therefore, is an attempt to preserve for posterity a specimen of Americana which in all likelihood will never be duplicated, for it is quite improbable that there will ever again be a legitimate bartender practicing under the protection of the Stars and Stripes. The work should thus be of considerable value to the scholar who wishes to study the manners and customs of the American people in the days before drinking became extinct, and the bartender a pariah.

Professor Thomas, in the preface to the first edition, has some very sound words on the social custom of drinking, which we quote:

> In all the ages of the world, and in all countries, men have indulged in "social drinks." They have always possessed themselves of some popular beverage apart from water and those of the breakfast and tea table. Whether it is judicious that mankind should continue to indulge in such things, or whether it would be wiser to abstain from all enjoyments of that character, it is not our province to decide. We leave that question to the moral philosopher. We simply contend that a relish for "social drinks" is universal; that those drinks exist in greater variety in the United States than in any other country in the world; and that he, therefore, who proposes to impart to these drinks not only the most palatable but the most wholesome characteristics of which they may be made susceptible, is a genuine public benefactor. That is exactly our object in introducing this little volume to the public. We do not propose to persuade any man to drink, for instance, a punch, or a julep, or a cocktail, who has never happened to make the acquaintance of those refreshing articles under circumstances calculated to induce more intimate relations; but we *do* propose to instruct those whose "intimate relations" in question render them somewhat fastidious, in the daintiest fashions thereunto pertaining.

The volume contains, as one might guess, formulae for the compounding of a large number of beverages now prohibited by law, including, of course, Professor Thomas's own inventions, Tom and Jerry and the Blue Blazer. Its historical value is enhanced by illustrations of typical

New York scenes of the 1870's, and also by portraits of the more illustrious bartenders of that time.

THE CORRESPONDENCE OF SPINOZA

Translated and edited, with introduction and annotations by A. Wolf.

Lincoln Mac Veagh, The Dial Press

$5.00 $5\frac{1}{2}$ x $8\frac{5}{8}$; 502 *New York*

An extremely well translated, edited, and printed edition of Spinoza's letters. It is a work of first importance to every philosopher and scientific man, because it makes it easily possible to read Spinoza, instead of about him, which has been the prevailing practice. The annotations are extensive and penetrating.

THE IMPOTENCE OF MAN ("*L'Homme Impuissant*").

By Charles Richet (Translated by Lloyd Harvey). T. Werner Laurie, Ltd.

7s. 6d. net $5\frac{1}{2}$ x $8\frac{1}{2}$; 150 *London*

The eminent investigator of ectoplasm here turns to philosophy. We regret to report that we can find no idea in the book which is not fully worked out in Epictetus or Lucretius. However, there may be some who will prefer the style of this volume; we shall stick to the classics.

VOL. IV, NO. 4 DECEMBER, 1929

THE QUARTERLY REVIEW *of* BIOLOGY

THE NUTRITIAL ACTIVITIES OF THE CALIFORNIA WOODPECKER (BALANOSPHYRA FORMISCIVORA)

By WILLIAM E. RITTER

University of California

INTRODUCTION

THIS paper is a portion of a more comprehensive study on the same general subject. Two objectives are aimed at in the whole study. One is to increase knowledge of the activational side of life in a particular avian species, certain of which activities are sufficiently unusual to elicit a rather unusual degree of popular interest. The other objective is to use the case for calling the attention of zoologists and others to the indubitable fact, as it seems to me, that here is a large and important segment of the phenomena of animal life to which relatively little scientific attention ever has been given or is now being given.

The closely related group of questions arising from the phenomena may be laconically worded thus: To what extent do animals make their heads contribute to their success in life? Stated a little more formally we may say: In exactly what way and in exactly what measure do animals use their heads toward solving the problems by which they are ever confronted in nature and which give rise to man's concept of struggle for existence? "Heads" is here used in no figurative sense—as a certain popular mode of expression might lead one to suppose. It implies the entire anatomical and physiological constitution of this portion of the animal organism. Certain members of the portion, viewed thus, spring naturally into prominence. These are the brain, the eyes and ears, and the mouth.

That the phenomena are not receiving the scientific attention they deserve may be seen by referring to two of the specialized fields of animal biology which would seem peculiarly the ones to which the phenomena should belong. These are *animal ecology* and *comparative psychology.*

Ecology is so recently differentiated within the science of living nature that the word had not yet got a place in the Century Dictionary of twenty-five years ago. Were we to take at its face value almost any definition of ecology, we might suppose it would include such a study as is here reported. For instance, "ecology is that branch of general physiology which deals with the organism as a whole, with its general life processes as distinguished from the more special physiology of organs" (Shelford, 1913, p. 32). This is certainly broad enough, and specific enough by implication, to include such a question as ours; yet I find scarcely a hint of any such question in the important book from which this definition is quoted.

The new book by Shelford, Laboratory and Field Ecology (1929), reached me too late to enable me to note statements in this important work that bear significantly on my view of mentality as a factor in animal ecology.

Nor does this type of question fare much if any better in very recent ecological writings. "Ecology is a new name for a very old subject. It simply means scientific natural history." (Elton, 1927, p. 1). Devoted to the ecology of animals as is the excellent book thus drawn upon, one might easily suppose our question would be appropriate to it. Yet apparently the author of the book does not think so. At any rate nothing in its pages indicates that he does. On the whole it seems that by a sort of tacit agreement, possibly on grounds of convenience, phenomena of the kind we are concerned with are excluded from this newly named old subject.

Working animal ecologists perhaps consider that phenomena involving the minds of animals, as our question does, belong properly to psychology and should be left to the special students in that realm. Nor does this seem unreasonable. Yet what has actually happened is that the phenomena are excluded from comparative psychology as this is now studied, and, so it appears, conceived, quite as thoroughly as from ecology. Almost without exception present-day investigators in this science have set as their goal the observation of animals under controlled conditions and so of necessity they have retired to the laboratories. This goal and technique, unquestionably important though they are, and fruitful of results in various ways, yet have no place in their programs of work for the class of phenomena here dealt with.

This definite, formal debarment of studies of this kind from comparative psychology of the modern period is specially well seen in the writings of C. J. Warden (1927 and 1928). But imprimatur itself is less convincing evidence on the point than that which may be gained from inspecting actual publications in the field. The paper I am now writing would be almost as much out of place in any current psychological publication (American at least) as in a botanical or geological publication. Were I to approach the editors of, say, *The Journal of Comparative Psychology* relative to publication, I should be prepared to receive with the adverse decision some such suggestion as that although the facts presented are rather interesting they pertain to geography or natural history, or, more specifically, to ornithology and not to psychology, even though a few of them have an indirect bearing on that science.

But while the phenomena in question do not come within the province of any really modern science (modern science as such science now defines itself) they are by no means neglected altogether. In fact they are receiving a good deal of attention in several countries by what may be called scientific amateurs. A considerable list of very painstaking field observers might be drawn up with mention of their contributions to knowledge of the general sort here treated. The United States and Germany would be well represented in the list; but the British Isles would almost certainly be the most extensively represented.

By way of illustrating from the side of publication what is referred to, I mention *British Birds*, edited by H. F. Witherby. The twenty odd volumes of this scientifically unsponsored journal are a real storehouse of observational facts similar to those recorded in this essay. The difference between the treatment of them by writers of the class here mentioned and that given them by me is that speaking broadly my standpoint demands that the phenomena be viewed more systematically and comprehensively and in certain aspects more critically than is required by the standpoint of most naturalists. For one thing my general view necessitates a technique of perfect balance (as near that as possible) between the qualitative and quantitative aspect of the phenomena involved.

Toward realizing this ideal on the qualitative side I have used terms that are as objectively and uncontroversially descriptive as can be selected. Words like instinct, intelligence, behavior, intention, thought, and reason, which so easily come into descriptions of animal activities, I have uniformly excluded. This I have done not because of any doubt about the general validity of these words or any prejudice against them, but merely from the wish to avoid raising theoretical questions from which I have wanted this treatment to be free.

On the quantitative side, although great exactness nowhere appears, I trust a certain regard for numbers and measure is recognizable at every turn.

Finally the investigation has been pursued and the results written about with the recognition constantly before me that the type of problem must necessarily be basically the same as that to which the nutritial activities of men give rise, even though men's activities are almost infinitely more complex than the corresponding activities of woodpeckers. Basically, I say, the problems must be of the same type for the unmistakable reason that their most fundamental aspects are the same. Food of some sort is certainly no more nor no less indispensable to men than to woodpeckers. Nor do the essentials of digestion, assimilation, and energy utilization differ fundamentally in the two cases.

Furthermore, the heads of the two animals surely have many activities in common. This is especially true as to the brain and the eyes. It is also true, with very important exceptions, as to the mouth.

Is it not, therefore, fair to suggest that studies of this type ought to hold much the same relation to studies on the activities concerned in the nourishment of man that studies on organs concerned in the nourishment of, let us say, the frog and dog, hold to studies on the organs concerned in the nourishment of man?

THE ACORN STORING OF THE CALIFORNIA WOODPECKER

So exceptional and striking are the operations of the California Woodpecker that they can hardly escape the notice of anybody who spends a little time in localities inhabited by it. This is especially true of its food-storing activities. As a consequence some information about its habit is widespread as well outside of, as in, California and all home countries of this and its subspecies. Many general writings of later years on bird life make some reference to the subject. If, however, one seeks information that is detailed and accurate he finds it to be meager indeed. So it has resulted, as usual in such cases, that various assertions about the matter which are "interesting if true" have gained wide currency. But "interesting if true" carries with it, here as usual, certain rather startling implications. If the assertions strike people as interesting it does not matter greatly whether they are true or not. Take one assertion that is specially prevalent about the food-storing performances of these woodpeckers.

Acorns, it is perhaps superfluous to say, are by far the most common objects stored. The favorite explanation of this is that what the birds are really after is not the meats of the nuts but the "worms" by which the acorns will become infested after they have been stored for a while. Just why this explanation is so popular is a question more of human than of bird mentality. It does not, therefore, fall within the purpose of this discussion. Enough to say that I have not found a single item of critical evidence in support of it.

On the other hand, the evidence that the meats of the acorns are eaten by the birds abundantly and regularly is ample. The contrary notion seems to have become a sort of folk story and so is nearly beyond the reach of science to correct. Some of the affirmative evidence is, however, significant for the present discussion. The consumption of the meats themselves has been observed by several naturalists, e.g., Bendire ('75), Henshaw ('21), and Ritter ('22); but the real place of the nuts in the birds' food supply could hardly be determined otherwise than by a study of stomach contents. Several such studies have been made, the most important of which are by Beal ('11) and Neff ('28).

From the examination of the contents of 84 stomachs, Beal found 53 per cent of the whole to consist of acorn material. These stomachs represented birds taken in every month of the year except February, April, and May. Twenty-three of the stomachs contained nothing but acorns; and twelve taken in November contained 93 per cent of nuts.

Neff's figures for the 73 stomachs examined by him differ considerably from Beal's, the most striking difference being the 49 per cent of "mineral matter" which he reports. "Acorns," he says, "were the commonest vegetable food, averaging 29 per cent for the year, and were taken more regularly than any other item of food."

The examination of the contents of three stomachs of the California Woodpecker, collected by Mr. W. H. Burt in Tehama County, California, October 30–December 2, 1928, gave the following results expressed in the form used in Food Habits Research, Bureau of Biological Survey, United States Department of Agriculture. The examination was made by E. R. Kalmbach.

1st specimen
Condition of stomach: ⅔ full
Percentage of animal matter, 1; of vegetable, 99; of gravel, etc., 30
Contents: Trace of unknown beetle, 1%; Fragments of a *Vespula* sp., 1%
A mass of acorn mast, 99%

2d specimen
Condition of stomach: full
Percentage of animal matter, trace, of vegetable, 100; of gravel, etc., 35
Contents: Jaw of an ant, trace: Acorn mast, 100%

3d specimen
Condition of stomach; full
Percentage of animal matter —; of vegetable, 100; of gravel, etc., 40
Contents: A mass of acorn mast, 100%

For interpreting these figures, it should be said that the quantity of "gravel, etc." mentioned means the portion by volume of the entire mass found in the stomach. E.g. the mass contained in stomach No. 1, was composed 70 per cent food material and 30 per cent "gravel, etc."

The well-nigh exclusive acorn diet of these three individuals is probably correlated with the fact that they were taken at about the height of the acorn season.

Attention should be called to the liberal amount of "gravel, etc." found in the stomachs and also in those examined by Neff. This suggests the possibility of a connection between gravel-eating and pebble-storing, noticed later.

INSECTS IN THE WOODPECKER DIETARY

Beal's formal statement that "larvae are almost entirely wanting" in the stomachs examined by him, "while acorns are eaten freely," is significant in its bearing on the general question of the bird's utilization of insects as food. It confirms the impression one gets from field observations that for the insect component of their dietary they depend less on the typical woodpecker method of digging for grubs than on the fly-catcher method of capture while both prey and themselves are on the wing. And this again agrees with the great general activity of this as compared with any other woodpecker.

That the several kinds of insects which, in larval and other stages are known to infest the acorns are also frequently eaten by the birds is undoubted. But this is no evidence that the birds do not eat the acorn meats, nor that the insects are the main object of the storing. The bird's food requirements are almost certainly what has led to the storing activity; and whatever in the acorn complex will contribute to that end may properly be said to be explanatory of the activity.

The cursory study I have been able to make, with the help of my entomological colleagues, Professors E. O. Essig and C. W. Woodworth, of the insect population of the acorns shows clearly that this is of itself an interesting problem collateral to the one I am concerned with, but altogether too complex for any but a professional entomologist to handle successfully.

But the fact that the meats of the acorns and not the insect inhabitants of them are the chief utility to the birds must not be taken to imply that acorn meats are eaten to the exclusion of insects. As a matter of fact, insects enter largely into the dietary of the birds. But to a large extent the insects consumed are flying ones caught while in flight. This woodpecker is almost as exceptional among its kind for its fly-catching activities as for its storing activities. Its performances in this connection constitute a subject of study in itself and are outside the scope of this article.

HOW USEFUL IS FOOD STORING?

My interest in the storing phenomenon exhibited by these woodpeckers dates from about 1907 or 1908. Quite casual at first, my attention to it has gradually increased until during the last decade I have devoted all the time to the subject that other more formal duties would permit. The freedom from official obligation of the last two years has enabled me to make rather careful though far from adequate observations on this aspect of the bird's life over most of its range in California. As a consequence I now feel that the problem is pretty well "staked out" in my mind, my notes, and my photographs and so is ready to be followed into its many details. More intensive field work, supplemented at various points by experiments, would undoubtedly bring added light on numerous questions raised and as yet only partly answered.

The aim of this article is to present the facts relevant to the following aspects of the general phenomenon: Assuming that the storing activity has arisen as an adaptation in the more general food-getting activities of the species, (1) What, if any, evidence is there that this unique activity (unique as compared with the food-getting activities of other species of woodpeckers) gives this species special advantage over other species? (2) How effective is the activity when considered in detail and on the supposition of its being fundamentally a special activational adaptation?

THE WOODPECKERS AND THE OAKS

So thoroughly dependent are these woodpeckers on the genus *Quercus* that nothing approaching a full answer to the questions asked is possible apart from a considerable study of this genus of trees throughout the bird's range. This woodpecker is bound to the oaks almost as closely as any species of parasite is bound to its host. But even so there is variety enough within the quercine genus utilized by the avian species to give the woodpecker a good deal of chance for variety in its food-getting activities and in its life generally.

Viewed from the standpoint of the "web of life," now so important a tenet of all biological naturalists, the California woodpecker must be looked upon as the avian species (not merely picidean species) which has surpassed all other avian species in utilizing for food the acorn crop of this particular geographic and arboreal region. In doing so this woodpecker has brought itself into close dependence on the oaks not only for food but in various other ways, notably in its reproductive affairs. Furthermore, this dependence on the oaks has resulted in dependent relations of the birds with various other species of trees and other objects, as wire-line poles, fence posts, and human habitations.

And finally the bird's quercine association has brought it into special relations, largely competitive, with various other species of animals. Among these competitive animals the California jay (*Aphelocoma californica*), and crested jays (*Cyanocitta stelleri*), and the California Gray Squirrels (*Sciurus griseus*) are specially to be mentioned since they appear to be the chief, though by no means the only, depredators on the stored acorns. These marauder species have to be noticed because security of the stores against them depends to a considerable extent on the way the storing is done (e.g., Ritter, 1921). A comprehensive treatment of the bird's relations with other animal species resulting from its storing activities would have to include a consideration of the uses to which men have put the acorn crop. For instance that these nuts were a chief element in the food supply of many of the California Indians is well known. And acorns have been and are a considerable factor in the hog, sheep, and turkey industries of California. Here as everywhere the web of life, if followed far enough, turns out to include man in one way or another more often than otherwise in some very practical way. But this aspect of the general problem outstrips the aims of this study.

GEOGRAPHICAL DISTRIBUTION OF THE CALIFORNIA WOODPECKER

So fundamental is the relation of the California woodpecker to the oaks that the suggestion naturally comes of a map of the region to show the distribution of these trees. But such a map would not be of much value as an aid to the present discussion unless it contained various details that are only partially worked out in the field, and are not yet reduced to map form. The details referred to concern various facts of ecological association, some of the most important of which for this study are too local to be cartographically represented except on maps of large scale. The following brief general statements aided by a very general map, figure 9, will serve the present needs. By a rough estimation, based on data contained in *The Silva of California*, by W. L. Jepson, on Jepson's personal help, and on my own field work something less than 50 per cent of the area of California may be counted as occupied by species of oaks and consequently as being the habitat of the California woodpecker. This gives the species approximately 70,000 square miles of territory within the limits of this State. And this nearly covers the case, since the species extends beyond these limits only to a short distance northward, into Oregon, and southward into Lower California.

The acorn-storing woodpeckers of Lower California have recently (J. Grinnell and H. S. Swarth, *The Condor*, Vol. 28, July, 1926, pp. 176–178) been recognized as two subspecies, *Balanosphyra f. martirensis* (northern part of the peninsula), and *B. f. angustifrons* (south end of the peninsula). Although these birds are storers, the fact that they present slightly diminished head sizes, especially in the beak, as compared with the Californians proper, suggests differences of some sort in the storing habits. But I know of no observations to prove this; and my own studies have not extended into this territory.

The north-south range of the California woodpecker is thus something more than a thousand miles. Altitudinally its range is from the sea coast to elevations of 4,000, 5,000, and even 5,500 feet. These ranges in latitude and elevation imply several different arboreal associations, some of which differ sharply as affecting the requirements of the woodpeckers. This point will figure in portions of this discussion.

Coupled with this exceptionally varied range of the species is the fact of its slight migratoriness. Typically the birds are segregated into groups of larger or smaller numbers, the locations of these being determined by the more or less sharply group-wise distribution of the oaks. This distribution of the oaks is in turn largely dependent on the precipitation and stream courses. There is very little in California corresponding to the oak forests of more humid regions.

These groups, some of them particularly, are remarkably constant in numbers and areal boundaries. Year after year, decade after decade, and probably century after century they remain much the same. The question of how much intercourse and interchange there is among them is important but we have almost no information on it.

ADVANTAGES OF THE STORING HABIT

Now we turn to the first of our formal questions, namely that of the special advantages, if any, that accrue to the birds, from the storing habit. There are two outstanding facts concerning the species which are closely correlated with this habit, and may justifiably be interpreted as benefits resulting largely from the habit. One of these facts is that the groups may flourish in localities which constitute remarkably different environments as compared with the environments surrounding most woodpeckers.

To illustrate, compare the set of conditions surrounding the two groups designated in my notes as the Ojai group and as the Palomar group. These are both exceptionally and about equally populous and flourishing. The Ojai group is in the small Ojai Valley, about 50 miles from the coast at Ventura, its elevation being 900 feet. The temperature here ranges from a maximum of 119°F. to a minimum of 13°F. with a mean of 61°F. The mean annual precipitation is about 24 inches, this being all rain and confined almost entirely to the winter half of the year. The oaks here are the Valley oak (*Quercus lobata*) and the Coast Live oak (*Q. agrifolia*). There are few trees of other species. The shrub and annual vegetation is also of moderate development. The Valley has been intensely agricultural and horticultural for nearly or quite a half century.

The Palomar group is well toward the southern end of the state in San Diego County on top of a long, broad mountain, the group's elevation being about 5,500 feet. The summer-winter range of temperature is from 100°F. to 9°F. with a mean of about 64°F. The region has a mean rainfall of 50 inches, most of which is winter rain, though rains in late summer are frequent. Heavy winter snows and drenching fogs are common. The prevailing oak is the Black oak (*Q. Kelloggii*) but the Maul oak (*Q. chrysolepis*) is common, its acorns being, secondarily to those of the Black oak, an element in the food supply of the birds. Several species of conifers come into the arboreal association, the most important of which from the woodpecker standpoint are the White fir (*Abies concolor*) and the Incense cedar (*Libocedrus decurrens*). Furthermore, the shrub and annual plant vegetation is varied in kind and luxuriant in growth for California.

It will thus be seen that in these two localities, we have to do with environmental conditions the differences in which would hardly be greater for equal areas of the United States bordering the Gulf of Mexico to the south, and the Great Lakes to the north. Yet as already said, populations of this woodpecker flourish the whole year through and year after year in these localities. Several other equally contrasted pairs of groups have come under my observation, for instance in the Visalia district of the San Joaquin Valley, elevation 334 ft. and the Yosemite Valley of the Sierra Nevada Range, elevation about 4000 feet. Also a colony in Mendocino County of northern California, and a seaside colony in Santa Barbara County 650 miles away in southern California.

While I would not attribute the species' unusual adaptiveness as thus exhibited to its storing habit alone it appears certain that to it and its correlated habits the adaptive phenomenon is largely due. It would take us beyond the purposes of this article to go into this matter fully; but one item is so relevant to the point that it must be noticed.

WOODPECKER SOCIOLOGY

Heretofore, we have spoken of the groups of individuals into which this species is so largely segregated, and have referred to the sharp localization of many of these. Looking more closely we find conditions which justify our speaking of the groups as settlements presenting some of the characteristics and advantages which appertain to settled as contrasted with nomadic human populations. Indeed the resemblances between these settlements of California woodpeckers and those of the California Indians are so unmistakable that the familiar name *rancheria* applied to the Indian settlements since the Mexican-Spanish period of California readily suggests itself. For some years I have recognized that to follow out in detail the social aspect of these woodpecker settlements is almost the major problem presented by the natural history of the species. But an execution of such a task will require much more extensive studies on various activational and structural phases in the lives of individual birds than have yet been made.

I would not give the impression that the distributional facies as one may say of the entire species, presents nothing else than these settlements. The truth is, a goodly number of individuals in many localities are seen where nothing of the settlement idea is recognizable. Rarely, however, according to my experience, does an individual occur quite alone. Whenever one is seen or heard, at least one other, usually more, may be expected. It is largely a question of oaks. Almost anywhere in California where there is a considerable assemblage of oaks if many of the trees are large a settlement of the California woodpecker is to be looked for. The size of the trees is an almost constant factor in the situation. Map the distribution of large oaks in the state and you map very nearly the settlements of these birds.

But there are very considerable areas of oaks of small and medium size. This is especially true of the Coast Live oak in parts of the coast ranges of mountains; and of the blue oak (*Q. Douglasii*) of the lower foothill belt of the Sierra Nevada. It is in these areas that the scattered or diffuse element of the population chiefly occurs. What the relation is between the scattered and the settled population is not at all well known.

RESIDENTIAL HOLES

In almost all cases the trees which furnish the birds with acorns and those used for storage are likewise the residences of the birds. This is especially so when, as often happens, the same tree both yields the acorns and serves as a granary for them. In other words relatively safe and permanent dwelling-places and relatively ample and ready-at-hand food supplies are in close proximity, not merely for a short breeding period, but throughout the year, and year after year.

Concerning what such interlocking of needs and activities means for animal life generally, we know a good deal, but not enough. Particularly are we poor in observational knowledge of such needs and activities during the incipient stages of highly complex modes of life and social organization.

In the case of this woodpecker we have some, though inadequate, observations on the breeding activities. But with these we are not now primarily concerned. The question that does concern us is whether and to what extent the birds use holes made by themselves as places of refuge against storms, cold, animal enemies and so forth.

Although observations under this head are few such as we have are to the point. They show conclusively that the holes are thus used more or less. The most definite published statements on the subject I have found are by Wheelock (1904) and Grinnell and Storer (1924). The former tells us that the birds "return to the same nest tree year after year, but usally excavate a new cavity, frequently utilizing the old as a shelter for the male on stormy nights." (p. 378). While this statement lacks particularity in several respects, the author's experience as a field observer makes it weighty as far as it goes. Referring to certain nest holes under their observation, Grinnell and Storer say: "Individual birds used these for roosting places at night in December, 1914, only one bird occupying each hole." (p. 341).

Mr. Frank A. Leach, though not considering himself a professional naturalist, has long been interested in various aspects of natural history. The grounds of the Mount Diablo Country Club, where Mr. Leach has resided for years, contain one of the finest groves of Valley and Live oaks in the Contra Costa region. This implies a large, flourishing settlement of California woodpeckers.

Mr. Leach has accumulated a large fund of information about the birds. Bearing on the point before us, he writes: "I have frequently seen as many as eight or ten woodpeckers retire in one nest-hole as the dusk of evening marked the closing of the day. Some of these abiding places are used year after year." (Leach, 1925). From correspondence Mr. Leach has furnished me more details about the matter.

Valuable information under this head is due to Mr. C. W. Michael, who for some years has been the postmaster of the Yosemite Valley. Both he and Mrs. Michael are experienced field observers. One of the fruits of their observations on the California woodpecker is quoted from a letter by Mr. Michael of January 12, 1929.

> In reply to your query of January 10, I can say that the California woodpecker does use the nest-hole, or a hole especially drilled for the purpose, as a sleeping chamber and as a place of refuge during storms. I have seen two birds come out of a sleeping hole in the morning and I presumed that they had spent the night together in the same hole. You know that the California Woodpeckers are not particularly early risers. Three birds had a nest-hole in the oak at my door and on more than one occasion I was down stairs early to watch the birds come forth. The three birds, two males and a female, were apparently equally involved in this nest and I was trying to learn if all three slept together. I did not settle the problem as never more than two birds were seen to leave the nest in the morning, but during the day all three birds were seen to go in and out of the nest hole.
>
> Often in the late fall a California woodpecker has been found at work drilling a hole. Now certainly he is not drilling a nest-hole at this time of year. Probably the bird is young and is making ready to spend his first winter.
>
> Up the road a ways there lived a pair of woodpeckers: we called them the "wealthy Melanerpes" because they were the pair that had the vast store of acorns in the bark of two great yellow pines. Their sleeping chambers were about sixty feet above the ground. Each bird had its own hole; the holes were about two feet apart, one above the other. These holes caught the first of the morning sunlight and often on cold mornings when we passed the birds were poking their heads out of the holes and chatting to one another. On rainy days too these woodpeckers were usually to be found looking from their doorways.
>
> In the dead limb which overhung one of the walks in the Valley three woodpeckers had a nest. When the young had flown the limb, which was considered as a menace to the public, was taken down. Immediately the woodpeckers set to work and drilled two new holes a little lower down in the remaining stub. These new holes were used as winter sleeping quarters.

That some other species of woodpeckers use nest and perhaps other holes as places of refuge is well known. Mr. Michael states that the Hairy, the Willow, the Lewis, and the Flicker do so. But in none of these species is there any such permanent and ample supply of food right at or near the places of refuge. The combination of advantages with which the California woodpecker has provided itself is what makes its case exceptional.

It is certain, then, that the holes into which the birds enter are not exclusively nesting places. They are also residential places of more or less permanence. And to some extent holes appear to be made for residences and not merely for breeding purposes.

Another thing about the holes may have a bearing on their efficiency as places of refuge. This concerns their position on the trees. Numerous references are made to nest holes in stubs of dead trees, wire-line poles and the like. This implies that such holes are on bare, exposed, upright surfaces. Undoubtedly holes thus located are not uncommon. I have seen such myself. However, I am quite sure these are not the most usual locations.

Quoting again from Wheelock:

> The hole is placed "usually on the under side of a large branch at some distance from the trunk." Several observers confirm this, and it accords with my own experience. So far is it the rule where the woodpecker settlements are most flourishing, that I have come to expect nest holes thus located, and rarely is my expectation amiss. Particularly is this the case where the Valley oak (*Q. lobata*) is exclusively concerned as in many parts of the San Joaquin and Sacramento Valleys; or where the Live oaks (*Q. agrifolia* and *Q. Wislizenii*) are almost exclusively concerned, as in some places, e.g. the sea-side Hope ranch at Santa Barbara; or, finally, where Valley and Live oaks intermingle, as in various parts of the Contra Costa, Santa Clara and Napa valleys. Nor are the nest holes restricted to decaying or even dead parts of the tree. Often they are in limbs or inclined portions of main stems that are alive, and, seen from the ground below, appear quite "sound."

When the tree association consists of the Black oak (*Q. Kelloggii*) and the Yellow pine (*Pinus ponderosa*), or the Incense cedar (*Libocedrus decurrens*), or the Silver fir (*Abies concolor*), so that the trees used for storing are other than those which furnish the acorns, the residential holes are less closely confined to the oaks and less likely to be on the under side of limbs. That residential holes situated on the under sides of large limbs or inclined trunks are specially well located for protection against storms is obvious.

It seems, then, justifiable to conclude that the relatively settled mode of life of these woodpeckers, dependent primarily on their food supply, has contributed importantly to enabling them to flourish about equally well over a geographic and ecologic range that is exceptional if not unique. This we have been stating in the specific terminology of ecologic associations.

We may now state it in the terms of life zones. Of two settlements about equally populous and vigorous, so far as I can see after having observed them rather attentively, one is at Visalia in the lower Sonoran zone while the other is on the floor of the Yosemite Valley in the transition zone.

SIZE OF POPULATION AS MEASURE OF SUCCESS IN ADAPTATION

The second fact I take as evidence of special usefulness of the storing activity is the abundance of individuals of the species, as compared with any other species which inhabits the same area either as a whole or as any "ecologic niches" within that area. It should not be forgotten that in almost any geographic area as large as that occupied by this woodpecker, local differences occur which on the one hand are unsuited to the species concerned, and on the other hand are suitable for other even closely related species. This is especially true in an area so topographically and latitudinally varied as is the state of California. It is partly this sort of thing that has led to the conception of ecologic areas or "niches" e.g. Grinnell (1914, p. 91) for general discussion and illustrations of this conception.

Seven other species are entitled to consideration under this head: The Red-shafted flicker (*Calaptes cafer collaris*); the Lewis woodpecker (*Asyndesmus lewisi*); the Downy woodpecker group (*Dryobates pubescens*); the Nuttall woodpecker (*Dryobates nuttallii*); the Hairy woodpecker group (*Dryobates villosus*); the Red-breasted sapsuckers (*Sphyrapicus varius*); and the white-headed woodpecker (*Xenopicus albolarvatus*).

In not many aspects of zoology is there greater lack of reliable quantitative information where such information is important than in that of numbers of population. This lack is largely due to the difficulty of census taking for most kinds of animals. The difficulties are surely real and in many cases well-nigh insurmountable. However in my opinion this difficulty is not alone responsible for our meager knowledge under this head. A perhaps equally influential factor has been an insufficient urge from recognition of the bearing of this problem on other still larger problems. For instance, in cases in which the number of individuals of a species or some regional segment of a species is seen to be important from the hunter's or nature lover's standpoint census-taking studies have been made with considerable success.

So far as I am aware zoologists have given little attention to number of population as a criterion of the relative success of kindred species and hence as measuring the degree of their adaptation. Particularly has the matter been neglected insofar as success depends on the activities, as contrasted with the structure, of individuals. The prevalent conception has been that the numbers of each and every species are controlled by the available food supply. All species are practically unlimited in reproductive capacity and hence are always crowding their means of sustentation whether this be plentiful or scant. Given times or places of great abundance and up go the numbers to meet it. Per contra, given times or places of great scarcity and down go the numbers correspondingly. This is held to be the "law" for any species just as much as for any other species.

THE ACTIVITIES OF ANIMALS AS A FACTOR IN THEIR WELL BEING

The question of whether the way each particular species has of utilizing its sustentative resources cuts any figure in situations as actually presented appears to enter exceedingly little into the problem as zoologists have conceived it. Inevitably, however, if one approaches the general phenomenon of animal life with his view fixed chiefly on the total round of individual activities he can not avoid the queries, What exactly are these activities? What do they count for toward the well being of their performers?

These queries as applied to one set of the activities (the nutritional) of one species are central in the present study. Unmistakably the storing activity of the California woodpecker involves nothing so deviative from the general woodpecker type of action as to call out much if any structural modification. The bird merely uses its mechanism to somewhat different immediate ends from those to which its kindred use theirs. Consequently no inquiry is closer to our starting point than that of whether the modified use to which the bird puts its mechanism gives it any advantage over its kindred in their common struggle for life. And surely one test of the matter must be that of whether, assuming them all to be on an equal footing in inherent reproductive ability, our bird outdoes its kindred in bringing its individuals through the full cycle of their lives.

THE RELATIVE ABUNDANCE OF WOODPECKERS

No effort has ever been made so far as I know to estimate the total number of Californian or any other species of woodpecker. Nor have I attempted the task. What I have tried, as an initial step toward better efforts in this direction, is to estimate the relative abundance of the several species in the geographic area which includes the species with which I am primarily concerned. While I make no pretense of having approached numerical exactness, the results justify, I am confident, the assertion that the numbers of this species distinctly exceed the numbers of its two nearest competitive species, and exceed by many times the numbers of the five other species listed above as belonging to the geographic area of the California woodpecker.

A few words must be spoken about certain liabilities to error due to peculiar conditions under which the numerical estimates have to be made. One of these is the fact that the tree associations favorable for this woodpecker are particularly favorable for human habitation. This brings it to pass that birds and men are thrown together by nature's arrangements more obtrusively than in the case of any other woodpecker, even if not more than in the case of any other native bird except the House Finch (*Carpodacus mexicanus*). Over and over again in many parts of California larger or smaller villages, country homes of city dwellers, golf courses, and farm residences are located as they are because of the fine development of Valley or Live or Black oaks. And these are exactly the places most favorable for settlements of this woodpecker. Among the most prized occupants of many a California door-yard are a few or several splendid oaks. So it happens that thousands of people in the State are more or less familiar with these birds, not from any special effort, but because environic conditions force it on their attention. It is this that credits the bird with being the most "sociable" of all our woodpeckers.

Add to this tendency to natural juxtaposition of humans and woodpeckers, the bird's unique food habits, its noisiness, its striking color displays and its open air flight, and we have a combination of circumstances favorable for recognizing and so for estimating numbers of individuals that does not hold for any other species. Numerical estimates must make due allowance for these encouragements to error.

My presentation may begin with the information from observations other than my own. A questionnaire seeking data on various aspects of the birds' activities was sent to a number of members of the Cooper Ornithological Club selected with reference to their residential distribution in the woodpecker's geographical area. Of the two questions designed to gain information about population, one asked for the species of woodpeckers occurring in the informer's locality. The other was, "What do you judge to be the order of abundance of these species?" All who answered were persons considerably experienced in observing birds, several of them highly accomplished in this way. There were eighteen answers to these two questions. Fifteen of these gave the California woodpecker first rank. The other three gave this place to the red-shafted flicker (*Colaptes cafer* subsp.). Furthermore, the flicker was assigned second place by five persons and the Lewis woodpecker (*Asyndesmus lewisi*) by one person. These estimates correspond pretty well with those derived from conversation with some of the best of our local ornithologists. That the flicker is next most numerous in the area as a whole seems probable from the available data. However, in the opinion of Dr. H. C. Bryant, one of the most widely experienced of California field zoologists, the flicker outranks the California woodpecker in the area.

But the assignment of first rank to the flicker by three of my questionnaire informants does not so much imply a general disagreement with the others as a difference of abundance dependent on localities. To those who have given any attention to woodpecker life, the statement is hardly necessary that although flickers are genuine woodpeckers in most of their structures and activities, in certain respects they are quite apart from their ordinal kind. So largely is their food obtained from the ground, notably from ants and other ground-inhabiting insects, and so little from trees, that their ecologic niche is quite different from that of other woodpeckers. To make an interesting story short, while the California woodpecker is mainly restricted, because of its food and food-habits, to certain ecologic areas within its geographic area, the flicker is able, because of its food and food-habits, to live not only in the same sub-areas occupied by the California, but in many other sub-areas where the California cannot live. Wherever nesting places are available, this typically implying trees, there flickers can and do thrive.

The only other possible claimant to populational equality with the California woodpecker is the Lewis. In some localities at some times this species far outnumbers the California, e.g. Bryant (1912). And since acorns are eaten by it to a significant extent, it becomes a sharer so far with the California in the latter's ecologic niche. But the Lewis is sharply different from the California in its general nutritional and correlated activities. Indeed as thus viewed the two species are nearly the antithesis of each other. While the California represents the acme of settled life and social intercourse in the order of woodpeckers, the Lewis represents the roving, individualistic life at almost its climax. If therefore the success of the picidean species inhabiting this part of the world is partly measurable by number of individuals, the three species here noticed would be entitled to the highest rank with, however, the California woodpecker distinctly in the lead.

This statement marks off at once activity problems for these other two species comparable with the problem under treatment for the California. But we can do nothing with them here.

A WOODPECKER CENSUS

I now present my own populational studies.

Since both sight and sound are essential modes of observation in field work of this kind: and since it is not always possible to be sure that an individual heard is another than one seen, it is often important that the mode of identification should appear in the record. My record of a trip to the Diablo Country Club, February 8, 1928, will be used as a sort of measuring-stick for the records in general. The observations entering into this record are particularly useful in this way because exceptionally fortunate in having been made by two observers (Mr. Frank A. Leach and myself) and in the number of species observed at the same station during the same brief period.

The record stands: California woodpecker, twenty-five at least (seen or heard). Flickers, four or five (seen or heard). Red-breasted sapsucker, one (seen). Nuttall woodpecker, one (seen). This numerical standard for the California woodpecker will refer more to density of population than to actual numbers, and will be on the basis of the number here estimated (25) in approximately an hour's observing over approximately a square mile of area.

Before considering the mass of records a brief statement is necessary about the way the field-work is carried on. The aim is to cover as much as possible of the geographic area of the California woodpecker. This implies that considerable of the territory traveled must be through places where the birds do not occur at all, or only sparsely or sporadically. This will be readily appreciated from what has been said about the dependence of the birds on oaks, and the character of the distribution of these trees. Travel is by automobile. As I am seated with the driver, who handles the vehicle with sole reference to the work in hand, stops and little off-the-road trips are readily made in response to what the constant look-out suggests. By this means many stops are made for examining localities where either the birds are obviously present or the general conditions are favorable for them. But stops are by no means alone in yielding information.

Birds and their work are often seen and entered into the notes without the automobile's coming to a standstill. From this mode of operation it results that two sorts of stations may be conveniently recognized: namely, those at which considerable time (from an hour to a day or more) is devoted to the observations; and those at which some though not much (less than an hour) of time is spent. These two kinds of station may be designated as "defined" and "undefined." Working in this way brings it to pass that a presentation of the data in tabular form is not profitably possible in the present stage of the investigation.

The records of a round trip of 800 miles through the interior valleys of the Coast Range of Mountains to Humboldt Bay north of San Francisco Bay, August 3–11, 1927, will be examined first. This set of records contains fifteen defined stations. At the three northern-most stations located well within the country of the Coast Redwoods (*Sequoia sempervirens*), no California woodpeckers were found; and from resident observers of birds the information was gained that the species does not occur here. The most abundant woodpeckers, according to these observers, are the Hairy and the Downy. The Flicker is common and the Red-breasted sapsucker not rare.

At all but one of the twelve other stations the records show the presence of the California. But at only three was the abundance comparable with the Diablo standard. At one of these three, that near Willits, there is a settlement almost on a par in numbers and thrift with the Diablo settlement. The favoring tree association here is of the Black oak-Yellow pine type. No other woodpeckers were observed. Another of the three stations just referred to is at Vichy Springs. Though the woodpecker settlement here is distinctly less populous than the Diablo settlement it seems to be well established and flourishing. Four Californias were seen at one time on the same tree, and certainly a goodly number of others were in the vicinity. One Flicker was heard and, doubtfully, one of some other species (Hairy?) was seen. The dominant tree association is the Black oak and Oregon Oak (*Q. Garryana*) and the Digger pine (*Pinus Sabiniana*).

The last of this group of three stations was in the vicinity of Lakeport on Clear Lake. This is primarily a locality of Valley oaks in association to some extent with the Common Cottonwood (*Populus Fremontii*). The presence of Cottonwoods I note particularly, as these trees are here used for both storing and nesting, which is rather exceptional. Although the number of Californias was considerable it seemed to fall distinctly short of the Diablo standard. No other woodpeckers were observed. None of the other nine records of this series show numbers or associative conditions which justify using the term settlement in connection with them. From one to a few—two or three—individuals were observed. No other woodpeckers are mentioned as having been observed directly; but the work of sapsuckers, in no instance fresh, was noticed at several stations.

A concluding statement certainly well within the bounds of the data is that although in the territory covered by this trip the numerical ratio of California woodpeckers to Flickers is distinctly less than that of the Diablo standard (about 5 to 1) the preponderance of the former over the latter is not in doubt.

WOODPECKERS IN THE SACRAMENTO VALLEY

The group of records next to be analyzed pertains to a round trip of 440 miles through the Sacramento valley to Red Bluff, at the northern portal to the valley. This trip was taken October 28 to November 1, 1928. It had the advantage of two observers instead of one, the second being Mr. W. H. Burt, an assistant and graduate student in the University of California. Mr. Burt's thesis work on the anatomy of woodpeckers makes him an especially valuable helper.

Eight defined stations and many undefined ones figure in these records. A general statement of importance that can be made is that in the northern, or Red Bluff, part of the territory, the Flicker was almost if not quite as abundant as the California; and that the Lewis was not far behind the Flicker. This estimate agrees with that made by Dr. Joseph Grinnell and Dr. J. Linsdale who did field work over much the same territory in January, 1929.

The considerable stretches of the Blue Oak (*Q. Douglasii*) in this region, consisting of trees that are scattered and not large, are not very favorable for the California woodpecker. The only approach in such places to the settlement form of life of the birds is in the rather few localities where the Digger pine is associated with the oak.

At four of the eight stations there are settlements comparable to the Diablo standard in seeming permanence and activity, and somewhat comparable to that standard in density of population if not in total numbers. These stations are at Joyland near Red Bluff, Orlando, Woodland, and Benali, all north of Sacramento, the last only a few miles away. At two of these, Orlando and Benali, Flickers were in evidence, five or six seen at one time at Benali. The Orlando station deserves special mention from being narrowly limited by its dependence on a tree association which in turn is narrowly limited by a flat-land river course—in this case Stony Creek, a branch of the Sacramento river. The association is of Valley oaks and Common Cottonwoods. There are many settlements in this type of locality in California. They are specially interesting from being favorable for the study not only of the population problem but several other problems connected with the social life of the birds.

Besides the California, the Flicker, and the Lewis, which figure largely in this set of records, the Nuttall and Willow Woodpecker come quite prominently into the picture. The Nuttall is specially to be mentioned, a total of at least a half dozen having been observed. The records of the Lewis, the Nuttall, and the Willow belong almost entirely to the numerous undefined stations. At the stations of this class, the general statement to be made is that so far as they are concerned, the California, the Flicker, and the Lewis were so nearly on a par as to numbers that it would be unjustifiable to say either surpassed the others. But at the four stations mentioned as having settlements of the Californias, their numbers undoubtedly surpassed the numbers of any other species. For this set of records, then, the conclusion is that the California surpasses though not greatly, its nearest competitors, the Flicker and the Lewis.

WOODPECKERS IN THE YOSEMITE VALLEY

The records of a trip to the Yosemite Valley, November 30—December 2, 1928, will next receive attention. Populationally viewed this trip was specially significant in two items. First it afforded a good chance at the question of numbers in the Valley itself. Second, it gave an opportunity for special attention to the woodpeckers of the Blue oak belt of the Sierra foot hills. The trip had again the advantage of Mr. Burt's ability as a field observer.

Personally, I devoted most of my time in the Valley to the woodpecker settlement connected with the grove of splendid Black oaks extending from the Plaza to the Yosemite Lodge. The birds were very active, though little storing was going on. The difficulties of census-taking in these settlements were impressive. The question of how many times the same individuals are being counted, hustling from tree to tree as they usually are, if visible at all, is surely a difficult one. Allowance being made for this and other difficulties, I can not doubt that I observed, either by eyes or ears, twenty-five individuals during a two-hour watch in one small area.

As to numbers in the entire Valley I have no basis for judging beyond the facts that the birds are certainly present in various other places, but generally less numerous than in this place.

As to other species: A few Flickers—hardly a half dozen—were seen or heard. Burt saw one Nuttall and, doubtfully, one Downy. Although the Lewis, the Whitehead, and the Pileolated were present in the Valley at the time, according to Mr. Michael, we looked in vain for them.

Concerning Californias in the Blue oak zone, this trip enables us to assert that they occur through the whole width of it from the upper part in the Blue oak —Interior Live oak—Digger pine association, to the lower part where the oaks alone abound. According to the evidence obtained, the birds are considerably more abundant in the upper than in the lower part of the zone. Much storing in the pines was observed and a considerable number of birds were seen or heard. The low foot hill sub-zone, having oaks only, furnished considerable evidence of storing, particularly in dead trees and in fence posts, though no birds were seen—probably because of the brief stops made. No woodpeckers of other species were observed in the zone. A good opportunity, however, was found for examining some extensive recent work of the Red-breasted sapsucker.

WOODPECKERS IN SOUTHERN CALIFORNIA

By far the most extensive single piece of field work contributing to this study was made in June, 1928. This involved 2000 miles of travel, extending southward nearly to the Mexican boundary. It reached the middle elevation of the Sierra range at the Yosemite Valley and the Giant Forest. It crossed the Tehachapi mountains at Tejon Pass; reached the middle slope of San Jacinto mountain; the upper elevations of Cuyamaca and Palomar; and extended through the valleys and passes of the Coast Ranges from the Sierra Madre mountains to San Francisco Bay. My field notes include 37 defined stations and a large though uncertain number of undefined stations. It is consequently obvious that a detailed examination of all these records would be a formidable consumer of time and space.

Fortunately, the character of the material is such that we can extract the essence of it with even less attention to details than was given the records of the Eureka trip for instance. What makes such a treatment possible is the fact that in this total of records the California woodpecker overtops all other species in numbers to such an extent as to render a detailed presentation quite unnecessary.

I will speak first of the results as they concern species which are to some degree numerical competitors of the California, namely, the Flicker, the Lewis, the Hairy and the Downy. The numbers of these appearing in the records are so small as to arouse suspicion that there is something wrong. Was the observing or the recording badly done? Or, perhaps, was the country traveled specially unfavorable for all woodpeckers except the California? Or, again, was the scarcity of other species due to the time of year? My greater interest in, and familiarity with, the California than with other woodpeckers may have played some part in the results—as may the country traversed and, possibly, the season.

Whatever the explanation here are the facts: A half dozen Flickers figure in the records occurring at five widely separated stations. Two were seen at one station; one at each of two stations; and one was heard at still another station. At a fifth station the birds were surely present, whether one or two or, possibly, more, I could not be certain as they were in and out of their holes. A single Lewis only was seen with certainty, though probably one other at another station was seen in flight. One pair of nesting Hairys was definitely located. The single Downy seen was the result of a rather extensive search in several places especially favorable for it. Three nesting pairs of Whiteheads were located, two at one station and one at another. Much work mostly old, of sapsuckers and, presumably, of Hairy woodpeckers was examined in many localities. But owing to the uncertainty which prevails among ornithologists as to the identification of these species by their work it would be profitless to dwell on these observations.

These factual statements concerning the numbers of other species may serve to show that at least I had this aspect of the population problem in mind and was on the lookout for comparative data.

We now examine this set of records more inclusively. The tabular form of presentation is possible here.

TABLE 1

Numerical results for California Woodpecker for 37 defined stations, field work of June, 1928, estimates referred to Diablo standard

Greater than standard	2
Approximately same as standard	5
Somewhat below standard	9
Much below standard	9
None observed	12
	37

More notice must now be taken of the fact that the "Diablo Standard" refers to density of population more than to actual numbers. The significance of this distinction is important. The point is well illustrated by the Diablo settlement itself. The numerical data entering into the standard are far from presenting the whole truth for this settlement. To illustrate. During the summer before (1927) that on which the standard was established, the Californias became destructive to the almond crop of a nearby orchard. As a consequence the owner of the orchard trained his shot gun on the offenders. Replying to Mr. Leach's inquiry about the number killed, the orchardist said that he kept no record but there were between one and two hundred of them. This orchard was not troubled by the birds the next summer, 1928, though the crop of nuts was fair. Accordingly none were killed by the orchardist. However between fifty and a hundred "in all probability" were killed in 1928 in the door-yard of a residence not far from the orchard. These were shot for amusement apparently, by the invalid occupant of the place, who was able to sit out-of-doors. In view, then, of the abundance of the birds at this place after such slaughter it seems necessary to suppose that normally the settlement here contains several hundred individuals.

Returning to Table 1, it will be noticed that two settlements are estimated as surpassing the Diablo standard. These are the ones at Ojai and on Palomar. The Ojai settlement, to which I devoted several hours divided between an afternoon of one day and a forenoon of the next, gave me the impression of easily surpassing any other I have ever seen in both density of population and total numbers. And as the area and the number of trees here are probably greater than those at Diablo, I conclude that the Ojai settlement surpasses the Diablo settlement in both. With the aid of Mr. O. E. MacBride, a teacher of science at the Thatcher school, who gives attention to the bird life of the region, I was able to see that in the Ojai settlement there are two rather well-marked subsettlements, one in the village itself, the other, two or three miles outside the village. Applying the Diablo measuring-stick, a total of two hundred individuals for these two subdivisions of the whole settlement seems to me a very conservative estimate.

Reference should be made to the fact that Mr. MacBride reports that a few Flickers occur in the Ojai valley; and that the Lewis comes there occasionally.

The other settlement ranking with the Ojai on the basis of the Diablo standard is the one on Palomar mountain, with which I spent part of an afternoon and the early hours of the following day. This surely equals the standard in density of population, and perhaps also in total numbers. But as I was not able to delimit the area and number of trees here as definitely as at the other two places, I am more chary about venturing any figure for the total population.

Concerning the five settlements appearing in the table as approximating the standard, the estimate has reference to the actual number (25) of the standard and also to density. I feel sure the estimate is more likely to be too low than too high. A list of these may be useful for further studies. They are: In Tajon Pass below Lebec; at Keen Camp on San Jacinto mountain and at Idyllwild on the same mountain; at a tiny place on a branch of the San Luis Rey river known locally as Shady Nook; and that in a small valley near Montecito. Probably the settlement in Yosemite valley and at Eden Dale farm, near San Jose, should be in this list; but preferring to err on the side of conservatism I have placed them with the nine grouped in the table as somewhat below the standard.

As to the remaining 21 stations appearing in the two columns of the table as "much below" the standard and "none observed," a good deal that might be said must be omitted as not important enough to influence the presentation as a whole.

Summarizing now on what this extensive set of records shows, we may say: The ratio of the California woodpecker to its nearest numerical competitor, the Flicker, is approximately the same for the set as that of the Diablo standard, namely five to one.

The conclusion for the whole territory included in the three sets of records here analyzed would be: While the numerical predominance of the California woodpecker over its main competitors, the Flicker and the Lewis, is distinctly less than over its nearest competitor of the Diablo standard, its predominance over these by two or three fold is hardly subject to doubt.

The question may be asked: Were all portions of the territory included in this survey to be examined as closely as were the portions especially favorable for the California woodpecker, might not the populational results be quite different? This is a legitimate question because many localities within the general quercine territory have no oaks at all or only such as are not favorable for these birds, yet do have various other kinds of trees and so are inhabitable by other kinds of woodpeckers. While it seems probable that the conclusions set forth would be altered to some extent by such examination, my belief is that the alteration would not be great and might affect the results in either direction.

ADVANTAGES OF THE ACORN STORING HABIT

At last, then, we are prepared to answer our question as to what if any advantages accrue to the California woodpecker over neighboring species from its nutritial activities. We have tried to show two ways in which it is a gainer. The habit enables the species to flourish equally well over a somewhat wider range of climatic and other environic conditions than can any kindred species with the doubtful exception of the Flicker.

Again, the rate of mortality of the species is believed to be lessened by its mode of solving its food problem. Evidence for this is found in the greater populousness of this than of related species which appear to be at least the equal of the California in rate of propagation.

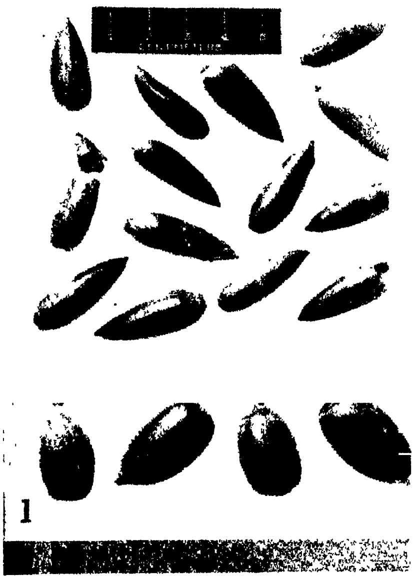
A case could undoubtedly be made for the view that the birds are influenced, probably beneficially, in most if not all their life activities. Their sexual and breeding activities are perhaps most notably thus influenced. One of the most striking attributes of the species as observed in the field is the extent and variety of its vocalization. Mention is made of this by nearly all writers. Viewing the "settlements" both analytically, i.e., as to the individuals constituting them and as wholes the question is close at hand: Have we not here phenomena that may justly be regarded as primordially social and cultural in nature? But this question reaches far beyond the bound set for this paper.

HOW EFFICIENT ARE THE WOODPECKERS?

We now pass to the second of our two initial questions: How effective is the activity we are concerned with? But is not the answer given to the first question also the answer to the second question? If it is really true that the activity is useful to the birds in the ways and to the extent indicated, is not this proof positive of the effectiveness of the activity? Undoubtedly it is. But while the result for the first question is an answer for the second also, it is only a partial answer. The answer to the first question is the answer to the second only insofar as the California Woodpecker's nutritional activities are compared with the same activities of *other woodpeckers*. The answer to the first question gives no direct information about the efficiency of the action as considered *within itself*. From the answer to the first question we get no light on the effectiveness with which the activity accomplishes the ends *in detail* which it obviously accomplishes *in general*. The effectiveness of all the activities of living organisms has to be judged partly by the extent to which each particular act accomplishes the end for which the class of acts is performed. Driving the blood to all parts of the body is the purpose of the contractile activity of hearts, and if on any account this activity is performed imperfectly blood distributing is inefficiently done and the possessor of the imperfectly acting heart suffers. That the hearts of *A*, *B*, *C*, and *D* act efficiently is no assurance that the heart of *E* acts thus. Nor is the fact that *A*'s heart acts efficiently today assurance that it will so act tomorrow. So is it with any functional activity of any organic being.

Enough results of the detailed studies on the storing activities of these birds will be presented to bring out sharply two divergent types of fact concerning their efficiency as just defined. First, the activities show a considerable degree of pliability with reference to different conditions under which they are performed. They are to a considerable extent adaptive within their own class as well as between their class and the class of nutritional activities of other woodpeckers. But, second, side by side with this adaptiveness of the activities in certain respects there occur striking failures of adaptiveness in other respects.

Evidence of four ways in which this intrinsic adaptiveness manifests itself will be briefly discussed: (1) in sizing the holes made for individual acorns to correspond to different sized acorns; (2) in selecting those acorns which from size and shape can be most conveniently managed when nuts differing in this respect are concerned; (3) in a measure of selection of storage places on the basis of the relative ease with which the storage holes can be made; (4) in shelling the nuts, whereby the halves into which the meats readily di-



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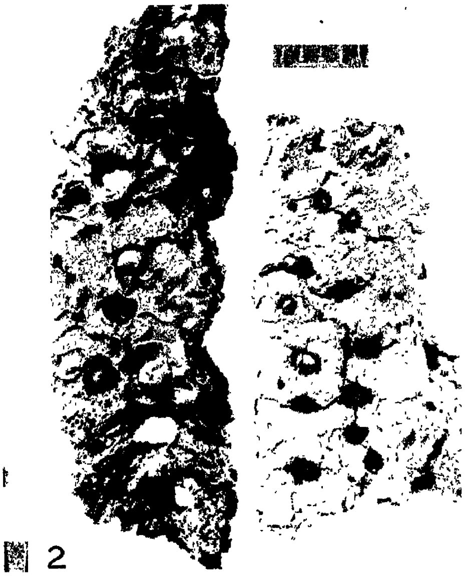

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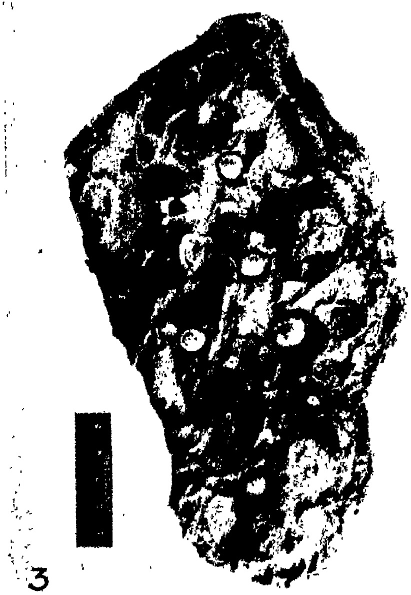

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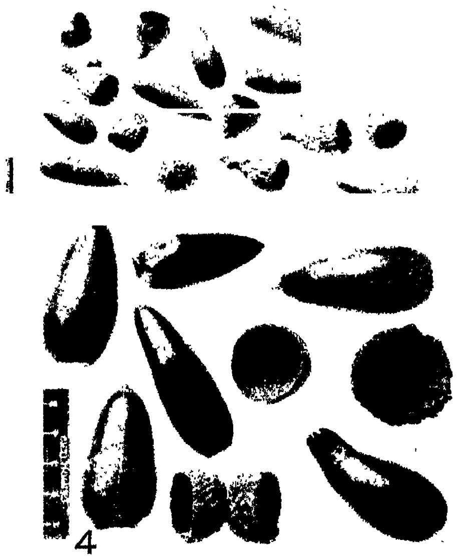

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FIG. 1. ACORNS OF BLACK OAK (*a*, LOWER) AND LIVE OAK (*b*, UPPER) TO ILLUSTRATE DIFFERENCES IN SIZE AND SHAPE

FIG. 2. BARK OF (*a*, LEFT) YELLOW PINE WITH LARGE HOLES CONTAINING ACORNS OF BLACK OAK; AND OF (*b*, RIGHT) SYCAMORE WITH SMALL HOLES CONTAINING ACORNS OF LIVE OAK

FIG. 3. BARK OF YELLOW PINE WITH LARGE HOLE CONTAINING ACORN OF BLACK OAK, AND SMALL HOLES CONTAINING ACORNS OF LIVE OAK

FIG. 4. ACORNS OF VALLEY OAK (*a*, LOWER), AND LIVE OAK (*b*, UPPER) SHOWING COMPARATIVE SIZE AND SHAPE

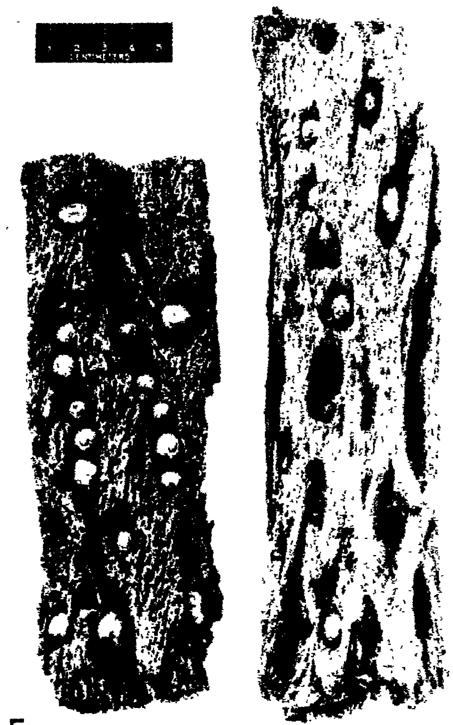

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FIG. 5. BARK OF EUCALYPTUS ROBUSTA (*a*, RIGHT) SOFT, CONTAINING ACORNS STORED MOSTLY IN HOLES; AND (*b*, LEFT) E. SIDEROXYLON, HARD, CONTAINING ACORNS STORED MOSTLY IN NATURAL FURROWS

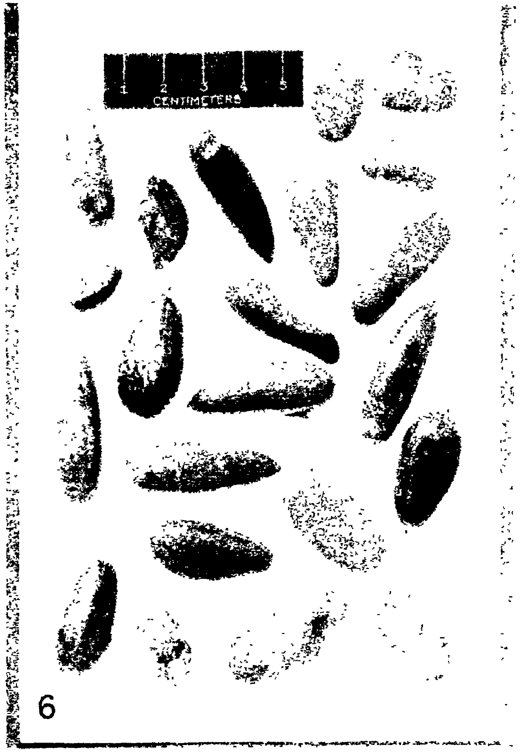

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FIG. 6. ACORNS AND PEBBLES COLLECTED FROM THE GROUND WHERE THE NUTS HAD FALLEN, SHOWING CONSIDERABLE RESEMBLANCE BETWEEN TWO KINDS OF OBJECTS

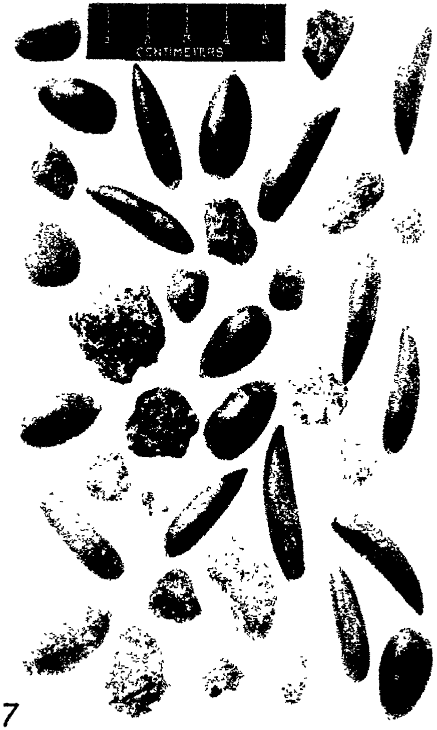

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FIG. 7. ACORNS AND PEBBLES COLLECTED FROM THE SAME TELEGRAPH POLE WHERE THEY WERE STORED BY THE WOODPECKERS, SHOWING LITTLE RESEMBLANCE

vide can be more effectively managed than the whole nuts can be. These we examine seriatim.

ADAPTATION OF SIZE OF HOLE TO SIZE OF ACORN

(1) That to a certain extent the size of the holes is made to correspond to the size of the acorns placed in them I have previously shown (Ritter, 1922, p. 116 f). For brevity's sake nothing more will be said about the evidence there produced. The presentation of new and more conclusive evidence can be facilitated by the photographs reproduced in figures 1, 2, and 3. Figure 1 is of acorns of the Black oak, 1 *a*, and Live oak, 1 *b*, these having all been taken by myself from the same storage tree. The average length and thickness, respectively, of the four Black oak nuts here shown is 30 mm. and 15.5 mm. These figures would certainly be nearly the same for great numbers of nuts of these oaks growing in localities and associations favorable for the birds. The same measures for the fourteen Live Oak nuts shown are 27.3 mm. and 9 + mm. There is much more variation, according to my observations, in the nuts of the Live oak, than in those of the Black oak. Nevertheless, these figures would be fairly representative for trees in localities and associations with which we are concerned.

Turning to the sizes of the storage holes and taking as samples those in the two pieces of bark shown in figure 2, we have the following figures: For the eight holes of 2 *a* the average is 14.5 mm. in diameter and for the thirteen holes of 2 *b*, 9.1 mm. Bringing nuts and holes together in the combinations that the birds make, we have this: The 14.5 mm. holes shown in Figure 2 *a* are for storing Black oak nuts of 15.5 mm. thickness and the 9.1 mm. holes of 2 *b* are for storing Live oak nuts of 9 + mm. thickness. While these statements are justified by the facts actually presented certain additional facts need to be noted, to dispose for one thing, of the difficulty that the holes containing the larger nuts seem to be actually somewhat smaller than the nuts. This may be due partly to the insufficient number of nuts and holes measured and to inaccurate measurements. But it is due more, probably, to the fact that in neither of these sets of measurements were the nuts and the holes from the same locality. The Black oak (large) nuts shown and measured are from Cuyamaca while the large holes shown and measured are from Keen camp on San Jacinto. The Live oak (small) nuts are also from Cuyamaca, while the small holes are from "Shady Nook" on a branch of the San Luis Rey river.

The justification for this criss-crossing of data as a convenience in presentation will be seen presently. It was indulged in from confidence that it would not seriously affect the results. My collections contain a large number of Black oak nuts that were actually taken from holes in the same bark shown in figure 2 *a;* and these differ too slightly from the four Cuyamaca specimens to have any recognizable influence on the quantitative results as presented. Similar remarks would hold for the Live oak nuts and the holes in which they occur.

It should be remarked that the samples collectable in this way are far less impressive than are the facts as seen in the field. This applies especially to the holes shown in figure 2. It will be understood that collecting specimens of bark from standing trees, live ones particularly, is not a simple matter. The dead, dry trunk from which figure 2 *a* was taken contained many—several scores at least—of holes similar to those shown.

A live sycamore near the one from which figure 2 *b* was taken contained easily several hundred holes, most of them having nuts, all of the Live oak. The uniformly small holes, each with its tight-fitting nut, was striking indeed.

We turn now to the specimen shown in figure 3. A glance is enough to reveal two distinct sizes of nuts and holes. The single large nut toward the right is a Black oak. The five smaller ones are Live oak. Everything is as it was while the piece of bark was on the tree—a yellow pine—the individual being the one from which the nuts measured, and shown in figure 1 *a* and *b*, were taken. As already noted, this specimen is from the middle slope of Cuyamaca, where Black and Live oaks and Yellow pines are freely mingled.

The evidence, then, is ample to prove that *within limits* the storage pits made by the California woodpecker correspond in size to different sized acorns stored in them. Before leaving the point attention should be called to the emphasis placed on "within limits." Although adaptiveness here is beyond question, it is far from perfect. But full discussion of this aspect of the subject must be omitted.

SELECTION OF EASILY HANDLED ACORNS

We now pass to the second way in which the activity shows adaptiveness: In a situation where acorns of different sizes are presented, those are to a certain extent selected which are of a size most easily handled by the birds. The acorns of two Quercine species utilized by the woodpecker at their maximum size are very near to, even if not a little beyond, the grasping capacity of the bird's beak. The beak is the only means the creatures have for "handling" (really for "beaking") the nuts; nor have the nuts anything in the way of a "handle" (beakle?) that can be grasped. The oaks referred to are the Valley oak, (*Q. lobata*) and Maul oak (*Q. chrysolepis*). Nuts of the first having a thickness of 26 mm. and a length of 48 mm. are not uncommon. And this species is one of the most commonly used of all the oaks. The normal opening at the tips of the mandibles as measured on one individual was 17.5 mm. Stretched to near the limit the measure became 25.5 mm. Thus it is seen that the larger nuts of the Valley oak can hardly be grasped whole. And the smooth, slippery surface of the nuts must increase the difficulty of holding the larger specimens.

I have no measurements of the acorns of the Maul oak; but certain it is that at their maximum they are at least as large as the largest of the Valley oak nuts. But this oak enters much less into the careers of the birds than does the Valley oak. I recall but two cases in which these nuts had been fed upon and only one in which they had been stored.

Since the selective action with which we are now concerned involves the Valley and the Live oaks almost exclusively, only these will enter into the rest of this discussion. Figure 4 *a* and 4 *b*, respectively, show clearly the size differences of these acorns. The evidence of selection as between the nuts of these oaks is that almost without exception where the two species mingle, I find the Valley oak used much more as granaries, while the nuts of the Live oak enter much more into the stored-up material. This is the rule to such an extent that it seems unnecessary to go into details. But the Diablo, the Ojai, and the Eden Dale Farm settlements may be mentioned as particularly good illustrations. Other possible explanations of the selection than that of size suggest themselves: May not the greater abundance of the Live Oak (smaller) nuts be the determining factor? It is impossible on the basis of present information to rule out this factor. The point involves, for one thing, the question of the relative fruitfulness of the two oaks. But according to Jepson (1910, p. 209) the Valley oak "bears more abundant crops of acorns than any other West American oak." My observations confirm this. Hardly, then, can greater abundance of the smaller nuts due to greater fruitfulness of the trees be a factor. But the possibility of more Live oak nuts from the presence of more Live than of Valley oak trees would have to be considered.

This, however, would not account for the fact that one often finds a Valley oak tree bearing a good crop of acorns stored with many Live oak acorns which must have been brought from distant trees.

Again it may be surmised that the Live oak nuts answer the food needs of the birds better than do the Valley oak nuts. For instance, is it not likely, one may ask, that the taste of the Live oak nuts is more to the birds' liking than that of the Valley oak nuts? This query is particularly relevant since the idea that the birds show a preference for the sweeter kinds of acorns occurs here and there in the literature. We surely have no evidence that one kind of acorns is better food for the birds than any other kind. As to the relative "sweetness" we have no criterion to go by but our own taste and for us the Valley oak nuts are distinctly sweeter. The evidence is, then, almost conclusive that the selectivity as to the kinds of nuts is on the basis of size.

SELECTION OF SOFT BARKED TREES FOR STORAGE

The form of adaptivity next to be noticed concerns the objects utilized as storage places. The relative hardness of the objects is the chief thing here. Nowhere does the point come out more definitely than in connection with those arboreal associations where soft-barked trees like the Yellow pine are mingled with hard-barked trees like the Black oak. In such cases I have yet to find an instance of departure from the rule that the pines are the granaries to the practically complete exclusion of the oaks. This is the more noteworthy because the oaks are abundantly so utilized in localities where there are no pines, as for instance where the Valley oaks or the Live oaks occur either alone or associated with each other. But even in these cases the rule as to hardness holds. Attention was called under the preceding heading to the fact that in Valley oak—Live oak associations, the Valley oaks are the chief storage trees. This is correlated with the greater availability in several ways of the Valley oaks for storing. For one thing the extensive ridge-and-valley structure of the bark of old individuals of this oak furnishes not only many nooks and crannies for storing with little or no bark picking required but also especially favorable conditions for regular hole drilling. The relatively even surfaced bark of the Live oak, to say nothing of its hardness, seems quite forbidding to hole making.

A striking example of this form of adaptiveness is presented by the resort of the birds to Eucalyptus trees for storing. Several instances of this are known, but far the most notable one known to me is near Santa Barbara and still nearer Montecito. Figure 5 *a* and *b* illustrates what has happened here. A rather extensive grove consisting chiefly of *E. robusta* and *E. sideroxylon* has been planted in a narrow valley in which Live oaks abound. The bark of *E. robusta*, 5 *a*, is thick, much ridged, and exceedingly soft and friable, while that of E. *sideroxylon*, 5 *b*, though likewise thick, is much harder. Both species are much used for storing. But, as a glance at the figures reveals, while most of the nuts stored in bark of *robusta* are in holes made by the birds, most of those stored in the bark of *sideroxylon* are in natural channels. Attentive comparison of the work done on these two kinds of bark discovers that whereas most of the preparation of the harder bark for storing has consisted in a little rimming out, so to speak, of the natural, narrow grooves to receive the nuts, most of that done on the softer bark has consisted in actual hole drilling.

When it is remembered that Eucalypts are very new comers, relatively, into the birds' environment, and that until their arrival no such sharp alternative as to soft and hard media for storage holes were presented to them, the case stands out strikingly as an example of adaptiveness in activity. For having my attention called to this interesting case and for the opportunity to study it, I am indebted to Mr. Ralph Hoffmann, author of a recent book (1927) on Pacific Coast birds.

Before leaving this topic it is desirable to refer more specifically to the use made by the birds of cracks of various kinds and in various situations for storage purposes. For instance the shrinkage cracks which develop extensively in dead and decorticated parts of trees, and in wire-line poles are much utilized. That this is connected in several ways with the general problem of the adaptiveness of the storing activity there is no doubt.

SHELLING OF ACORNS

The fourth and last form to be discussed of intrinsic adaptiveness exhibited in the storing activity concerns the shelling of the nuts. My attention was called to this by Mr. C. W. Michael, who seems to have been the first to observe it. Since this phase of the activity came to my notice I have been on the lookout for it. In two instances during my field trips in company with Mr. Burt we have found shelled and halved meats of acorns stored in deep cracks along with whole nuts. Almost certainly this was in both cases the work of the California woodpecker. But since Mr. Michael's observations furnish much the best evidence we have on the point, I confine myself to this source, giving most of it in the observer's own words as communicated to me by letters from the Yosemite Valley under dates of December 2 and 13, 1928:

"On the morning of December 2, 1928, I saw an individual California woodpecker, the same individual, and he was never out of my sight, gather and crack two acorns. This same individual was seen to store four half acorns. However, the dead limb which he used as a vice when hulling acorns was some fifteen feet above the ground and from where I stood I could not be positive that the half acorns that the woodpecker carried away and stored were already hulled acorns in the vice. . . . . In this particular case it was not the least difficult to follow the movements of the woodpecker under observation for he did not move far. He picked up acorns on the lawn, flew to the limb used as a vice, and then to the eaves [of a dwelling house] where he was storing. Never was he more than 100 feet from me." A few additional details are given in another letter. "The operation of gathering, shelling and storing the two halves was completed in slightly less than five minutes."

The entire process was followed in only one bird. But since at least ten others were at work at the same time, the storing act proper being seen in some of these, Mr. Michael felt sure that other individuals were doing essentially the same things. While, as stated, the performances most completely followed stored the nuts in the eaves of the building, other nuts were put into cracks between the shingles of the main roof. Although the observed facts are not sufficient to justify the assertion that the shelling and halving had as its direct, immediate end the storing of pieces in niches too small for the whole nuts, there seems no doubt that the pieces could at least be more easily handled than could the wholes. The tree concerned is the Black oak, the nuts of which, it will be recalled, are considerably larger than those of the Live oak.

Another point mentioned by Mr. Michael is that the nuts on the ground from which the birds were making their collections, were found to be splitting open in many cases—owing undoubtedly to the wetting they and the ground had received from the winter rains and snows. This fact, illustrative of a rule for fallen nuts this late in the season, must greatly facilitate the task of shelling. Along with these considerations it should be noticed that these birds seem never to swallow the acorns meat, shell and all, as is the way with some creatures, e.g., the Band-tailed pigeon and the Mule Deer. This means that opening the nuts in one way or another is part of the task of preparing the food. Undoubtedly this must come into the reckoning along with that of storing the shelled pieces. But even so a large measure of adaptiveness is unmistakable in the operation.

To sum up, the food storing activities of the California woodpecker manifest intrinsic adaptiveness in four particulars: in fitting storage holes for acorns of different size; in selecting nuts of convenient size for handling; in selecting storage objects on the basis of greater and lesser resistance to hole drilling for the nuts; and finally, in shelling nuts, thereby gaining advantages in managing parts of nuts instead of whole ones. This is the answer to our second primary question, that of the effectivensss of the activity when this is viewed from the inside. From the general nutritial standpoint it shows considerable effectiveness when its own particular acts are compared among themselves.

MALADAPTIVITY IN STORING

But fidelity to truth and fullness compels us to recognize that side-by-side with the observed facts which lead to the conclusion as stated there are other facts of quite different purport. Some of the most conspicuous of these will now be examined. I have discussed certain aspects of this matter elsewhere (Ritter, 1922, p. 109f, and 1928, p. 128f), using the term maladaptivity for the types of activity described. I will restrict the presentation here to three of the most positive types and give factual information gathered since the publication of the earlier discussions. These will be: (1) the storing of objects that are entirely useless as food: (2) the storing of valuable food objects where they can not be recovered by any means available to the birds; (3) the pecking of holes that are either unusable for storing or, though usable, are not used.

STORING OF OBJECTS USELESS FOR FOOD

(1) The following is a list of stored objects which up to now have been observed: acorns, almonds, hazel nuts, dates, Indian Corn, English walnuts, pecans, native California walnuts, seed capsules of the Eucalyptus, stones. The list is arranged with general reference to the usability of the objects as food. Acorns, of course, head the list and head it so pronouncedly as to leave no room for question that it is with these objects that the activity is primarily concerned. Almonds, occupying second place in the list, probably hold second place, now, among nuts as food for those of the woodpeckers that inhabit almond raising districts. But this, of course, could be true only for very recent times. There is considerable evidence that in some localities and perhaps in earlier years, hazel nuts were used quite extensively. The place of stones is necessarily at the other end of the list. But utterly useless as these are either as food or in any other imaginable way, the storing of them we now know to be rather common. For instance from my questionnaire and from various other sources I now have a list of at least ten instances where such storage has taken place. The phenomenon is then sufficiently characteristic of the storing activity to make it deserve careful study.

How does such an absurd perversion of a useful activity come about? The hypothetical answer which I gave several years ago was this: Assuming that acorns for storing are sometimes picked up from the ground, and that this takes place occasionally where the nuts have fallen in pebbly places (as is not infrequent) it is conceivable that the resemblance of some of the pebbles to acorns is so close as to lead the birds to mistake the one kind of objects for the other. To test this hypothesis has been one aim of my recent studies. During the last year the aim has been measurably attained. That the birds actually do collect nuts after they have fallen is testified to by so many observers that there can be no doubt about it, although gathering from the trees is the only mode I have personally observed. While on the Red Bluff trip in October last I found striking instances of acorns resembling more or less closely pebbles on the ground under the trees from which the nuts had fallen.

Figure 6 shows a sample of the collection made. While the reader will have no difficulty in distinguishing acorns from pebbles, neither will he fail to see considerable similarity between them.

Fortunately, not many miles from where this collection was taken an old wire line pole richly stored with both acorns and pebbles was found. This gave a chance to see how much resemblance there was between the two kinds of objects. Figure 7 shows the two mingled as in the previous case. No one can fail, I think, to see that acorns and pebbles of figure 7 resemble each other less than do those of figure 6. In fact the pebbles stored by the birds are about as unlike the acorns stored with them as could be gathered. This comes out more sharply on the samples themselves than in the photographs, since diversities of color as well as of shape and size figure in the comparison. The evidence, then, tends strongly to disprove my hypothesis that pebble storing is due to mistaken resemblance, if resemblance is understood in any detailed, critical sense.

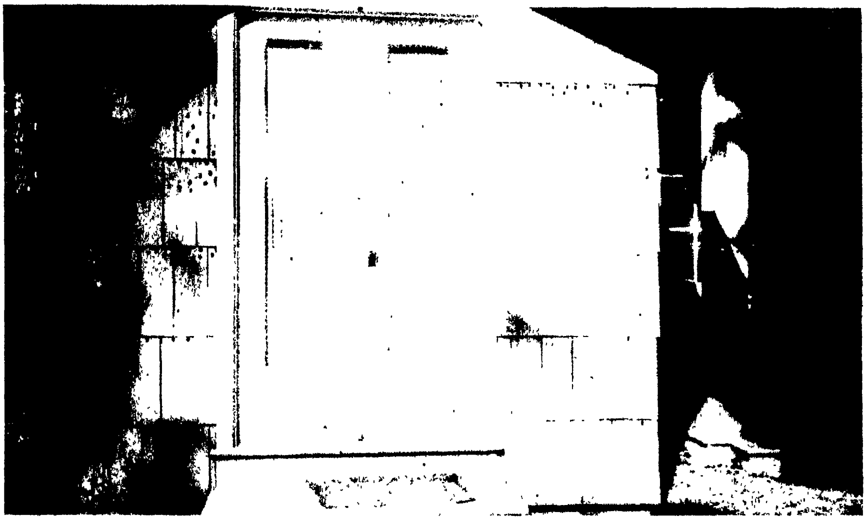

FIG. 8. PORTION OF END OF A COTTAGE AT MT. DIABLO COUNTRY CLUB SHOWING HOLES MADE BY THE WOODPECKERS, MOSTLY COMPLETE BUT SOME INCOMPLETE

Another explanatory hypothesis of the phenomenon is given by Henshaw (1921). He suggests that pebble storing is done in seasons when, or localities where, the acorn crop is more or less of a failure. Under such conditions the poor birds store pebbles as a substitute for nuts!

Still another possible significance of the phenomenon is suggested by the discovery that the stomachs of the birds may contain liberal quantities of gravel and other mineral matter. Perhaps the change from animal to rather hard vegetable food has been accompanied by the taking of a certain amount of gravel to aid in triturating the food—something after the fashion of the utilization of gravel by some graniverous birds. Should this surmise prove correct still another adaptation in connection with the acorn habit would have to go to the credit of this woodpecker. More field observations, supplemented if possible by experiments, are necessary for testing these guesses.

The whole problem of utterly futile activity by animals is here touched upon but does not enter into the aim of this paper. That here is an instance in which the real end served by an activity is entirely missed is so obvious as to need no dwelling upon. My only discursive remark on the subject is that the impression made on a free minded observer is that the birds have a general activity-set toward picking up objects and storing them away and that this is stimulated into action by almost any objects which are at all amenable to such action.

It is doubtful whether the seed capsules of the Eucalyptus and the almost stony hard nuts of the native walnut (*Juglans californica*) are more available to the birds as food than are pebbles. I should expect that objects of any kind whatever of manageable size, copiously strewn among fallen acorns from which collections were being made by the birds, would get a place in their garnered material. The phenomenon is, I take it, the same in general character as that of the great variety of absurd objects on which brooding birds will sit (see Kirkman, 1927, p. 863).

STORING OF FOOD WHERE IT CANNOT BE RECOVERED

We next consider the storing of good food objects where they can not be recovered. An instance in point is indicated in figure 8. The cottage here shown is on the grounds of the Mt. Diablo Country Club. The numerous holes appearing in the shingles, or shakes, are the work of the woodpeckers. This building is sheeted inside as well as outside. Consequently many of the perforations open freely into the space usual to this form of construction. What may happen in connection with the acorn storing business here tells its own story. The case is presented as a real example of what is not rare in California and is familiarly regarded as a joke played by the birds on themselves. Mr. Leach tells me that the wall of this cottage has been opened several times to remove the accumulated acorns; and that the quantity taken out may be well toward the bushel mark, the nuts being in various stages of decay or consumption by insects and mice.

An instance reported by Mr. John Ultringham, living in the country near Lodi, California, is even more to the point. The continued activity of the woodpeckers around a particular telephone pole attracted Mr. Ultringham's attention. Looking into the matter this is what he found. The pole bore a conduit pipe from which the wires had been removed. The birds were dropping articles into its upper end. Further examination found a pile consisting of acorns, almonds and walnuts under the lower end which opened a foot and a half or more from the ground. Thinking to test the "industry" of the birds, Mr. Ultringham put a fruit picker's bucket under the pipe. This was filled several times in the period during which he watched and emptied it. The nuts were not put where the birds could not get them in this instance. But what was gained by dropping their food through the pipe, assuming they expected to eat it at some future time, is hard to see. Although this story does not come from a woodpeckerologist, there is no reason to question it. So in keeping is it with much that the birds certainly do that they might well have done the thing reported, even if they didn't.

To give all the details of this sort contained in my notes would consume time and printer's material, beyond any informative value it would have. On one question which may be raised something should be said. Is this form of nutritial maladaptation restricted to situations which have been imposed, so to speak, upon the birds by the coming of man into it is not. From the abundance of such evidence I will present only two instances. One is furnished by Peck (1921). This I have referred to in previous publications, but it is sufficiently striking to warrant mentioning again. Although Peck's observations were on a different subspecies (*Balanosphyra f. albeolus*) and were made in British Honduras, the point under consideration is not essentially altered thereby, I am confident. The kernel of the case, stated in the observer's own words is: "I have seen a hollow pine tree with a cavity six or eight inches in diameter filled for a distance of nearly twenty feet with acorns dropped into a good-sized hole at that distance above the ground. Acorn-filled trees of this sort I found not uncommon. Sometimes an opening at the bottom showed the earlier acorns deposited completely decayed and crumbling to dust."

An equally natural but less striking instance of a like kind came to my notice at Keen Camp on San Jacinto mountain during my work there in June, 1928. Some of the bark of a dry pine stub (the one from which the piece shown in figure 2 was taken) had sloughed off entirely while other portions were so loose as to be separated from the wood by a considerable space. One of these pieces which was still adherent at its lower end some two or three feet down, had been abundantly punctured by the birds. Most of the holes in this piece went entirely through the bark. As a consequence the acorns put into these holes dropped down in the space between bark and wood. The accumulation of lost nuts, perhaps a quart, I happened to find from pulling off the loose slab of bark for a specimen.

ABORTIVE HOLES

The third and last form of uselessness of the activity concerns the holemaking itself. Here again to save time and space I will do no more than add to the evidence previously given in my *Condor* articles that great numbers of holes are made into which no acorns or anything else are ever put. The additional point in this aspect of the matter I will now emphasize is that innumerable of these uselessly made holes are useless from the simple fact that they are not made large and deep enough to receive the nuts. The point is illustrated in the photographs of the bepunctured cottage of the Diablo Country Club (fig. 8). It will be readily seen that the spots on the shingles vary greatly in size, some of them being only a little above visibility. A bit of evidence from this cottage is presented in tabular form (see table 2, page 482).

On this exhibit slightly less than 55 per cent of the holes are large enough to receive nuts. But this is certainly have not here wasted 45 per cent of their work. For instance in this case had I counted all the holes in all the shingles many would have shown what the 8th shows, namely all the holes full sized. Furthermore, as the table indicates many of the abortive holes were fresh. This means that later the birds may complete them. The percentage of old and hence presumably fully abandoned abortive holes is not here large. The whole instance is however truthfully illustrative of an extensively performed kind of futile activity. A good example is furnished by a wireline pole in the same neighborhood. This pole is thickly marked from bottom to top by the hole-making industry. There are certainly several hun-

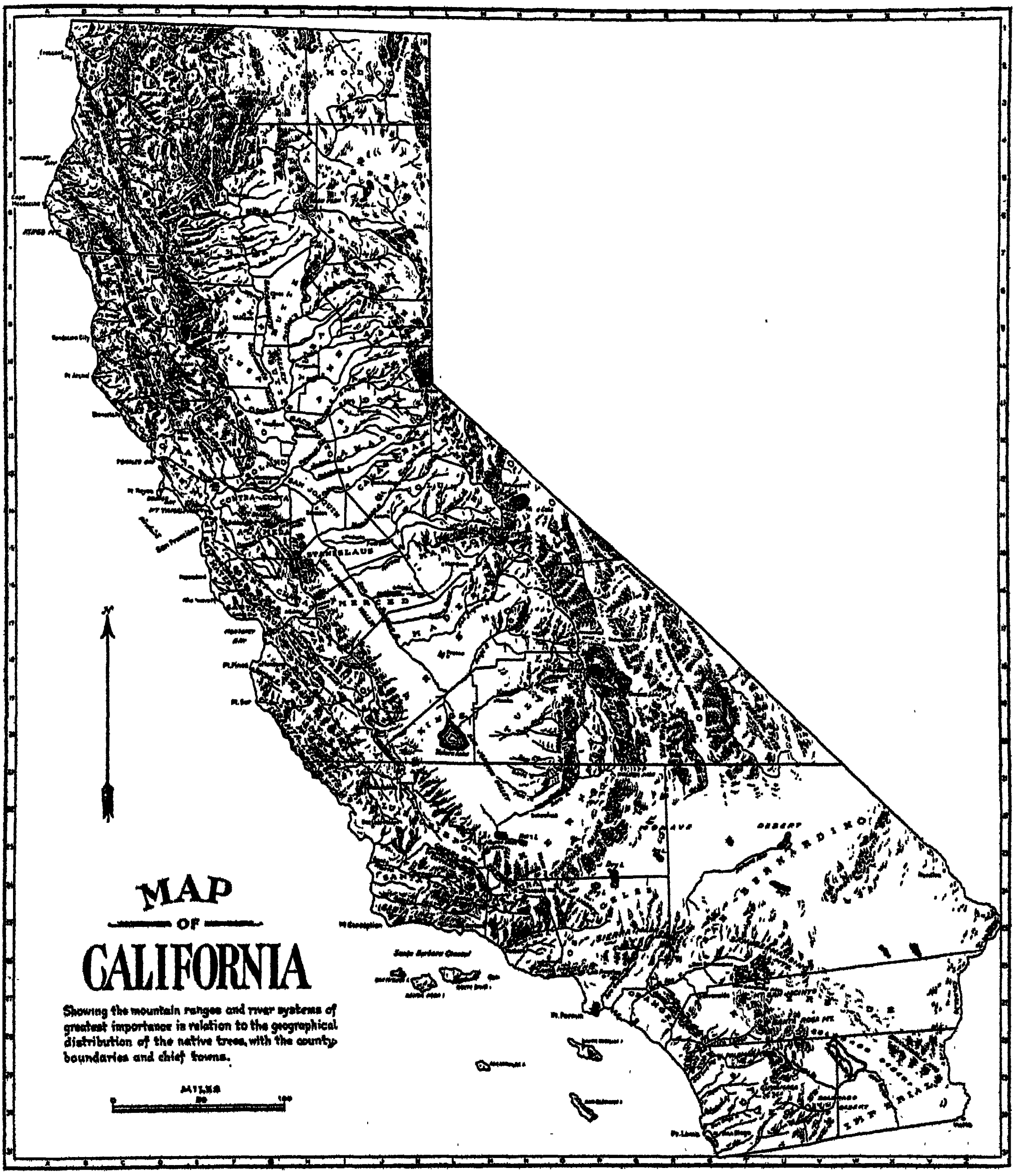
MAP
OF
CALIFORNIA
Showing the mountain ranges and river systems of greatest importance in relation to the geographical distribution of the native trees, with the county boundaries and chief towns.
MILES
0
50
100
CONTRA COSTA
STANISLAUS
San Francisco

Fig. 9. Map of California, After Jepson (1910)

dred of these marks. And certainly, too, less than half of them are deep enough or broad enough to admit even the smallest acorns. And all the work is old. There is nothing to suggest the possibility that the job is to be completed after a while. Yet the birds are all around here, undoubtedly alighting frequently on this very pole.

A customary view about the abortive holes is that they are unfinished in the sense that a ditch or a tree-planter's or a well-digger's holes in the ground must of necessity be unfinished part of the time. Or in particular situations such as this cottage presents, where people, dogs, cats, etc., are apt to come along, the supposition is that the birds were driven or scared away from their tasks. Another explanation favored by some naturalists is that such work is exploratory or trial. By this view it is placed in the category of the gold miner's prospect-hole or the oil man's prospect-well.

TABLE 2

SHINGLES	TOTAL NUMBER OF HOLES	FULL SIZED HOLES	ABORTIVE HOLES
1st	12	3	all old
2d	8	3	all fresh
3d	7	4	all fresh
4th	16	10	all fresh
5th	9	4	all fresh
6th	19	11	all fresh
7th	9	4	all old
8th	10	10	

But after allowance is made for explanations of this sort, it is, I believe, demonstrable that a great amount of activity performed not only by these woodpeckers, but by many other animals, is utterly futile judged on the basis of the obvious usefulness of the activity *as a type*.

The display of abortive holes in the Diablo cottage is no greater than can be seen in innumerable other cases where none of the above mentioned common explanations can be positively shown or even reasonably supposed to be operative.

The most convincing evidence for the contention that a considerable part of the hole-making activity of the California woodpecker fails to attain the end it typically does attain and so is adjudged futile, can be got by watching the birds at work.

I give a single instance from my Yosemite Valley trip of November-December, 1928. But preliminary to the narration reference should be made to Mr. Michael's belief that the woodpeckers of the Valley have largely abandoned trees as acorn storing places and have taken to wooden buildings, largely for the purpose, he believes, of utilizing cracks into which by a little enlarging the nuts can be thrust. I have considerable personal observational evidence confirmatory of this view. Certain it was that no tree storing was observed during my late visit, yet the birds were abundant and very active. And no small part of their activity was pecking—mostly on dead, dry, barkless branches of the Black oaks.

As seemingly typical of this work take the following from my field notes: "Bird working on side of a limb in full view. Five fresh pits in a row, one apparently large enough for a nut. None of the others deep enough. Bird worked alternately in two or three of these, then went away." There was nothing recognizable in the situation to explain the cessation of pecking. The bird was merely acting in a general way like a dozen or more others in the immediate vicinity. Certainly one can imagine that this individual, perhaps like others which had previously worked at the same pits (I was almost sure the bird watched did not begin any of them, at this "shift" any way) decided there was something wrong about the place. Or he can imagine that the individual went away to get something to eat or to do something or other with some other individual with the intention of returning after a while to finish the job. And several other more or less plausible explanations can be imagined. But since the case itself furnished no observational evidence for any of them, it seems useless to entertain them. Conclusive evidence that innumerable holes are started and never finished is supplied by the fact that weathering and other unmistakable signs of age are upon them.

SUMMARY

A final summing up of the results of this study may be given thus: California woodpeckers promote their own welfare as this depends on food by the use they make of their heads, in at least two ways: (1) they somewhat extend, as compared with neighboring species of woodpeckers, the range of their most vitally influential external conditions of life; (2) they somewhat reduce, as compared with neighboring species, their rate of mortality as shown by their increased ratio of adult population to their reproductive capacity.

This greater effectiveness of their nutritial activities as compared with those of neighboring species may be designated as *extrinsic evidence* of adaptiveness of the activities.

Attentive study of the activities discovers them to vary considerably with the somewhat varied external conditions under which the birds live. Four kinds of external conditions to which the activities conform more or less are presented in the study. This sort of thing may be designated as *intrinsic evidence* of adaptiveness of the activities.

But the studies which secure this intrinsic evidence of the activities' adaptiveness can hardly fail to discover sharp limitations to this adaptiveness. Three kinds of such limitations are presented. They are designated as *maladaptations* of the activities.

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THE CYTOLOGY OF GLANDULAR SECRETION (*Continued*)

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THE RÔLE OF THE CYTOPLASM IN SECRETION

For the cytologist, at least, the problem of the origin of secretory products is thus definitely located in the cytoplasmic area of the cell.

Bowen, 1924.

THE attempt to find a nuclear basis for secretion having eventuated rather dubiously, many workers have concentrated their attention on the cytoplasm. In some cases nuclear activity has been definitely eliminated, in others nuclear cooperation has been held possible or necessary. The earlier accounts of changes in cytoplasmic appearance accompanying secretion frequently speak only of a "mucous degeneration," or in other ways derive the secretion droplets from the general cytosome (Paneth ('88), Yamanouchi ('22), and many other references given on page 305). Such meaningless statements have long since been abandoned with the unfortunate exception of some holocrine glands, as already noted on page 304. It is now clear that a satisfactory explanation of the origin of a secretory droplet must be reduced to more concrete terms. To accomplish this, appeal has been made to practically all of the formed components of the cytosome, with results which will be reviewed in the following pages.

The granule doctrine

Das Grundgesetz des Secretionsprocesses also ist überall dasselbe: überall haben wir es zunächst mit den primären Granulis zu thun, ... ; die aus diesen primären Granulis heranwachsenden und heranreifenden Secretkörner liefern die specifischen Bestandtheile des Secretes.

Altmann, 1894.

Danach würde die erste Entstehung der Granula einfach darauf hinauslaufen, dass kleinste, metamikroskopische, lebende Teilchen einen gewissen Grad der Selbständigkeit erlangen und durch Assimilation, Wachstum und entsprechende Metathese ihrer Substanz sich in die histologischen Granula umwandeln.

M. Heidenhain, 1907.

Of the cytoplasmic structures we may conveniently take account first of the ultimate particles into which living matter is presumably divided, taking our departure from the granule theory of protoplasmic structure associated with the name of Altmann ('94). According to the granule doctrine, living matter consists of a congeries of discrete particles each of which is 'alive,' and can by hypothesis grow, divide, and differentiate itself into this or that cellular product. According to Altmann ('94), a secretory droplet arises by the mere growth of one such granule or bioblast, which eventually achieves the transformation chemically necessary for a particular secretion (compare also with the section on chondriosomes, page 488). This view has been developed by M. Heidenhain ('07), who derives secretory granules directly from the ultimate, submicroscopic, living particles or "protomeres," out of which he considers protoplasm to be constructed. His point of view is admirably stated in the sentence at the head of this section. Other workers (Müller ('96, '98) Noll

('01), Jurisch ('09); compare also Saint-Remy ('92)) have sought a similar escape from the difficulties of tracing the exact relation of a secretion to any previously visible component. Secretory granules have a disconcerting way of emerging into visibility apparently from nowhere—in which respect they but emphasize the universal sense of defeat which everyone must feel who attempts to account for the appearance in the cytoplasm of a formed component not previously visible. The obvious escape from such a dilemma is the assumption that a secretory droplet has emerged from a distinct formation which already existed in submicroscopic form. Thus is the whole situation deftly removed from the domain of cytological analysis, and we are left at the very threshold of the essential problem with a sense of utter futility.

That such an explanation should prove satisfactory to cytological workers is clearly not to be expected, especially when we take into account the obvious difficulties involved in the necessarily theoretical assumptions as to the ultimate structure of living matter. Most workers have, therefore, sought for a more tangible solution among the formed constituents of the cytoplasm. The results of this search must now be considered.

Protoplasmic fibrillae—The ergastoplasm

> On a admis qu'il [l'ergastoplasme] y participait directement ou indirectement. On l'a considéré comme un prézymogène, c'est-à-dire comme un premier stade chimique des grains de sécrétion définitifs. Mais aussi, n'ayant pu observer la transformation directe de l'ergastoplasme en matériaux de sécrétion, on lui a attribué une influence indirecte, et directrice dans l'élaboration de ces matériaux.
>
> Prenant, 1910.

When gland-cells—the vertebrate pancreas furnishes particularly good examples—are fixed in fluids characterized by the presence of mercuric chloride but containing no osmic acid, and are then properly stained, their cytoplasm is frequently found to contain fibrillar structures. These are primarily a characteristic of the basal end of the cell and their distribution is frequently limited to that zone; whence the term "Fussplasma" used by Jacobs ('28) after Frenzel; also called 'Basoplasma' by Roskin ('25), and basal protoplasm ('protoplasme basal') by Morelle ('27a), and many others. Such a fibrillar appearance seems to have been first clearly described in gland-cells by Eberth and Müller ('92), but the prior observations of Macallum ('91) should also be noted, and some workers credit the first description to Pflüger or R. Heidenhain at much earlier dates (e.g., Saguchi, '20a). These fibrillae were subsequently described in more detail by Solger ('94, '96, '98), who applied the name "basal filaments," and as the "ergastoplasm" of Garnier ('97, '00a, b) and Prenant (protoplasma supérieur) ('98–'99), their importance was much emphasized. In the years which marked the turn of the century, the resulting 'ergastoplasm theory' received a great deal of attention.

The exact morphology of the ergastoplasm has never been very clearly defined, and in the hands of various workers it has assumed several quite different forms. Most frequently, as the name given by Solger ('96) suggests, the ergastoplasm presents itself in the form of filaments (fig. 7*A*) (cf. Solger ('94, '96), Mouret ('95), Garnier ('97, '00a, '00b), Hammar ('97), Prenant ('98–'99), Mathews ('99), Theohari ('99), Saguchi ('20a), Lutz ('21), Krüger ('23), Roskin ('25), Jacobs ('28)) which were frequently supposed to be in some way related to the fibrillar cytoplasmic structure of Flemming's familiar theory (Solger ('96), Hammar ('97), Garnier ('00b)); while Saguchi ('20a) called them protofibrillae; and

Krüger ('23) thought the filamentous appearance was determined by the inward diffusing stream of fluid from the vascular channels. Others, however, especially among more recent workers, have considered the ergastoplasm merely as an amorphous, diffuse material located in the basal region of gland-cells (fig. 7*B*) and easily transformed into a fibrillar appearance by improper fixation (Bensley ('98, '11), Regaud and Mawas ('09a), Dolley ('25), Benoit ('26), Morelle ('27a)). Perhaps the ergastoplasm should include (e.g., Laguesse ('11, '24), Lutz ('21), and especially Morelle ('27a)) the various nebenkern-formations described by Nussbaum ('81) and many later writers and already discussed on page 320. The point which seems to have been relied upon to bring all these divergent structures under the heading 'ergastoplasm', is their common affinity for basic stains. Many earlier workers traced this staining reaction to a supposed contribution of nuclear chromatin drawn off from the nucleus by the ergastoplasmic threads (Mathews '99, Garnier '00a). Other workers describe the nuclear contribution in various terms (cf. Conte and Vaney ('02), Launoy ('03), Regaud and Mawas ('09b), Brinkmann ('12), Millot ('26)), while Dolley ('25) considers the ergastoplasm as equivalent to chromidia (see page 321), a relationship categorically denied by Lutz ('21). On the other hand, any relation to the nucleus has been absolutely denied in other instances (Limon '02, Lutz '21, Roskin '25, Jacobs '28). On the whole, the most tangible feature of the ergastoplasm seems to be its alterations in amount (and staining capacity) at different parts of the secretory cycle. Thus, in cells actively synthesizing secretory droplets, the ergastoplasm is fully developed while in cells

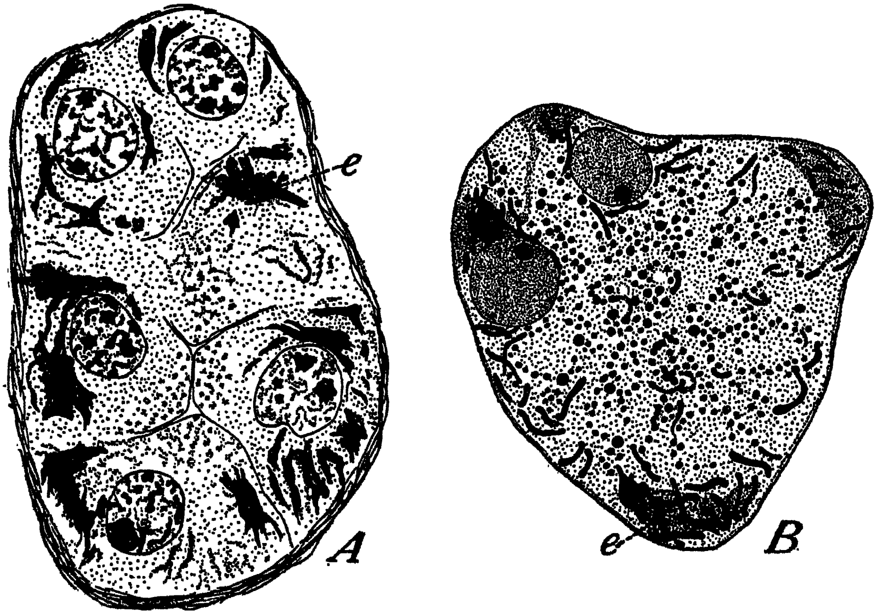

Fig. 7. The Ergastoplasm in Gland-Cells

A, fibrillar type in the submaxillary gland of man, from Garnier, 1900; *B*, amorphous type (rod-like bodies are chondriosomes) in the submaxillary gland of man, from Regaud and Mawas, 1909. *e*, ergastoplasm.

loaded with secretion it is greatly reduced or entirely absent (cf. Garnier ('00a, b), Prenant ('98–'99), Jacobs ('28), and many others).

Exactly how the ergastoplasm is connected with secretory activity has never received any very definite explanation, even from those who were its most ardent advocates. Almost no one has described an actual transformation of the ergastoplasmic fibrillae directly into secretory granules, a procedure definitely excluded by Eberth and Müller ('92), Garnier ('00a), and Regaud and Mawas ('09a) (but see Mouret ('95), and Theohari ('99)), although such a description of the fate of the nebenkern has been occasionally given. Usually the development of the ergastoplasm has been viewed as in some sense precedent to the synthesis of the secretory substance proper (Solger ('96), Garnier ('97, '00a), Laguesse ('99), Mathews ('99), Limon ('02), Bensley ('11), Brinkmann ('12), Lutz ('21), Dolley ('25), Benoit ('26), Jacobs ('28)).

The reduction of the ergastoplasm concept to a concrete statement is, therefore, a practical impossibility. The facts seem only to warrant the idea of an ill-defined substance of basophilic nature located toward the base of a gland-cell (the 'cell-portal,' Benoit, '26) and connected in some way with the production of secretory products. The very indefiniteness of the ergastoplasm-concept and the fact that it is so well demonstrated after technical methods certainly known to be destructive of cytoplasmic structure, early led to doubts of its status as a legitimate cell-element. The development of the chondriosome theory dealt the idea of ergastoplasm a very serious blow, and it was soon pointed out that in all likelihood the ergastoplasm was merely poorly fixed chondriosomes. In the end, Prenant ('10), himself one of the foremost proponents of the ergastoplasm theory, frankly admitted that this was probably the truth. Others have viewed the matter in the same light (e.g., Bouin ('05), Champy ('11), and Mislawsky ('13) (in part)), and Laguesse ('24) has developed a very complicated sequence involving a cycle of nucleolus-ergastoplasm- chondriosome- secretory granule.

Nevertheless, many recent workers have not accepted Prenant's surrender of the ergastoplasm, and the presence of a special basophilic or chromophilic substance is still believed by some to be coexistent with the quite different chondriosomes (Regaud and Mawas ('09a, b), Bensley ('11), Saguchi ('20a), Lutz ('21), Dolley ('25), Benoit ('26), Millot ('26), Jacobs ('28), Ma ('28)). Some of these workers (Saguchi, '20; Jacobs, '28) still interpret the ergastoplasm in fibrillar terms, but the majority opinion seems to be that it is an unformed material which is easily rendered fibrillar by fixatives which are too strongly acid. Fixatives of the type (non-acid) now accepted as essential for cytoplasmic study usually yield preparations in which the basal substance is not fibrillar. The essential facts were indeed largely grasped by Bensley as long ago as 1898, and the full rôle of the fixative has since been made known by several workers (Bensley ('11), Dolley ('25), Morelle ('27a)).

Whatever status, therefore, may be finally assigned to the ergastoplasm, it seems reasonably certain that the remarkable fibrillar structure of the classical accounts is of very doubtful reality. It appears more and more probable that two quite different things have been confused under the name of ergastoplasm. One of these is only a remnant of the poorly fixed chondriome and represents the fibrillar material as Prenant conceived it. To this extent the ergastoplasm problem comes more properly under the head of the rôle of chondriosomes in secretion (q. v., infra). The other is a specialized protoplasmic region in a gland-cell expressive of the special activity in the basal zone, where the incoming materials from the capillaries must be particularly concentrated, and where perhaps they undergo the first steps in secretory synthesis (Benoit, '26). Such activity is perhaps reflected in the distinctive staining capacity of the basal zone. To this extent the 'ergastoplasm' would represent one phase of the secretory activity of the cell as a whole, and in some such indirect rôle, if any, the ergastoplasm must now apparently find its interpretation. At all events it is at present clearly impossible to develop from the ergastoplasm any useful explanation of secretory origins. For those who might have some special interest in this problem, I might add that few subjects have been so adequately or frequently reviewed as the ergastoplasm, and the voluminous literature is discussed by several authors in much more detail than has been possible in this place; cf. Eberth and Müller ('92), Solger ('96), Garnier ('00a), Laguesse ('05–'06, '11, '24), Prenant ('98–'99, '10), Saguchi ('20a), Lutz '(21), Roskin ('25), Benoit ('26), and Morelle ('27a).

The chondriosome theory

> . . . . ce rôle du chondriome s'établit d'une façon très simple: les chondriosomes se transforment directement en grains de sécrétion.
>
> Hoven, 1912.

> una continuità materiale, . . . fra i condrioconti e quelli che abitualmente son ritenuti i prodotti dell'attività metabolica della cellula, non esiste.
>
> Levi, 1912.

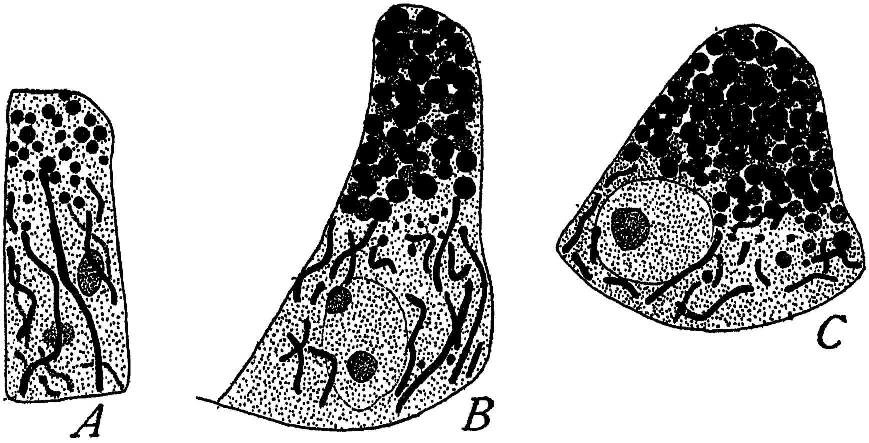

FIG. 8. STAGES IN THE SECRETORY CYCLE OF THE PANCREAS-CELL IN THE GUINEA-PIG SHOWING THE SUPPOSED DIRECT TRANSFORMATION OF CHONDRIOSOMES INTO SECRETORY GRANULES

From Hoven, 1912

Close upon the heels of the ergastoplasm theory, antedating it, indeed, in the work of Altmann, came the chondriosome theory, which for a few years achieved a remarkable vogue as an explanation of all histological differentiation. In accordance with Meves' theory, it was to be expected that chondriosomes would yield secretory granules. Indeed, as subsequently became clear, the granules (bioblasts) and 'vegetative fibers,' from which Altmann had derived secretory granules (refer to page 305), were actually chondriosomes, and thus Altmann had anticipated many of the later developments of the chondriosome theory. Specific investigation of the problem of the relation between chondriosomes and secretory granules eventually resulted in three quite different views of the situation. According to one view, early sponsored by Schultze ('11), and Arnold ('12), but particularly developed by Hoven ('12), Altmann's original account is corroborated. The chondriosomes in gland-cells were believed to fragment and the granules thus derived were transformed, with an accompanying increase in size, into definitive secretory droplets (fig. 8). As a necessary corollary, the amount of chondriosomal material was said to show a marked decline toward the end of the secretory cycle. According to the second view of the part played by the chondriome in secretion, the chondriosomes do not themselves become secretory granules, but act in some sense merely as selecting bodies or plasts in or on which the secretory materials are deposited (fig. 7*B*). This view was particularly developed by Regaud ('09, '11) as the "eclectosome" or plast theory, and a point of view in many ways similar was also expressed by Prenant ('10) and Laguesse ('11, '24). According to Regaud the chondriosomes are the organs on which are fixed substances destined for

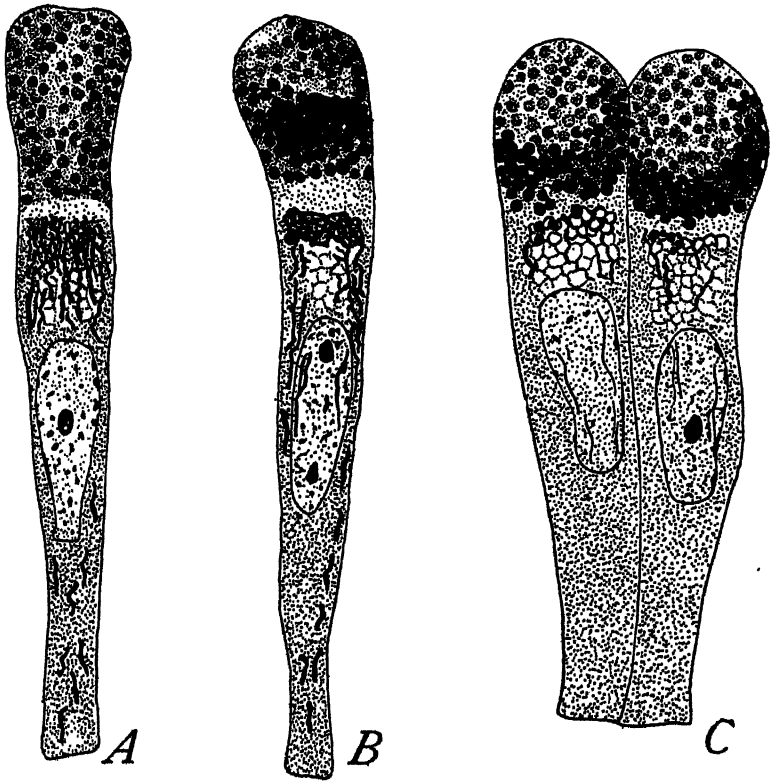

Fig. 9. Relation of the Chondriome to the 'Golgi Area' During Various Stages of Secretion, in the Stomach-Epithelium of the Axolotl

Successive figures show the gradual consumption of the chondriosomes in the building of secretory droplets. From Tschassownikow, 1927.

the chemical functioning of the cell; these organs concentrate the substances thus fixed, elaborate them and transform them into secretion-products." The third interpretation of the rôle of the chondriome in secretion is of very recent origin. Originally foreshadowed by the work of Saguchi ('20a), it has received support and more detailed development at the hands of Kull ('25), Morelle ('27), Tschassownikow ('27) and Urasov ('27, '28). It was also suggested as a possibility by Nassonov ('23), but definitely not supported by his later investigations; and Saguchi, in his original paper, apparently considered the material of the Golgi apparatus as also secretory in character. The adherents of this third viewpoint hold that the chondriosomes fragment, more or less as described by Hoven, but that the granules thus formed are subsequently modified by some action of the Golgi apparatus, becoming in the end the basis of the definitive secretory droplets (fig. 9). The details vary as given by the different authors, but the cooperation of the Golgi apparatus is, in each case, the essential feature. Here also may be mentioned the recent hypothesis of several Chinese workers (Lim and Ma ('26), Ma, Lim and Liu ('27), Ni and Lim ('28), Ma ('28b), and Ling, Liu and Lim ('28)), who believe that the chondriosomes represent a substance which is split into secretory material on one hand and Golgi apparatus on the other. This particular view is at variance with all other work on the nature of the Golgi apparatus, and to me at least seems untenable.

The view sponsored especially by Hoven has been supported in more recent years by a number of workers, for example Hauschild ('14), Schreiner ('16, '18), Beigel-Klaften ('18), Jirešová ('18), Takagi ('20, '25), Ma ('25), and Millot ('26). Of these workers, Schreiner (and also Saguchi, '20a) traces the origin of the chondriosomes to the nucleolus—a view which seems certainly incorrect, although very recently reiterated in slightly different form by Dehorne and Hosselet ('28b). Nevertheless, Hoven's interpretation has met with very serious criticism, particularly at the hands of Levi ('12), Mislawsky ('13) and Cowdry ('18); and other recent workers (Bremer ('13), Eklöf ('14), Key ('16), Calabresi ('19), Veratti ('22), Nassonov ('23), Benoit ('26)) have denied any direct transformation of chondriome into secretion. Chief among the reasons for this attitude is the fact that the staining phenomena, in which Hoven placed so much confidence, are no longer accepted as sufficient evidence of material continuity between a chondriosome and a secretory granule. I think it is fair to say that the direct origin of secretory granules from chondriosomes must today be definitely abandoned because of the impossibility of demonstrating any material continuity between a known chondriosome and a recognizable secretory droplet. It may also be added that the question of a fluctuation in amount of the chondriome synchronous with the secretory cycle, much emphasized by Hoven, is still entirely unsettled. Regaud and Mawas ('09a, b), Bremer ('13), Eklöf ('14), Grynfellt ('21), Takagi ('25), Lim and Ma ('26), Morelle ('27a), Tschassownikow ('27), and Urasov ('27, '28), corroborate Hoven's statement that there is a decline in the amount of chondriosome-material as the secretion accumulates, while Key ('16), Calabresi ('19), Nassonov ('23), Noel ('24), Jacobs ('28), and Parat ('28) deny any significant fluctuations. It is in any event a question whether any fluctuations which might occur must necessarily be given Hoven's interpretation.

Regaud's idea, on the other hand, has much to recommend it on theoretical grounds, and has been adopted in one sense or another by several recent workers (Eklöf ('14), Calabresi ('19), Grynfellt ('21), Noel ('23, '24), Laguesse ('24), Laguesse and Debeyre ('25), and doubtfully Benoit ('26) and Ziegler ('27)). Nevertheless the demonstrable facts have not proved sufficiently positive to afford a real basis for this view and it has not achieved any wide acceptance. Its failure to win support may also doubtless be traced in part to the serious doubts which have been thrown on the chondriosomal nature of the plastids in plants, structures which were used as prototypes for the eclectosome theory.

As for the view sponsored by Saguchi, Morelle, and others, although supported by the work of several competent observers, it must be said that the derivation of secretory substances from the chondriosomes does not seem to be in harmony with most of the recent studies of the Golgi apparatus in gland-cells (cf. page 503), nor is it in harmony with the conditions in the spermatid, where the acrosomal vesicle (see beyond) develops without any morphological relation to the chondriome. And the recent work of Parat ('28) on the earliest secretory vacuoles (vacuome) offers definite and very strong evidence against the interpretation of any chondriosomal derivative as the direct forerunner of secretions.

I may add that the whole problem has been reviewed extensively by Duesberg ('12) and Cowdry ('18) who, on the basis of the older data, arrived at opposite conclusions. Their original papers should be consulted for a much more adequate statement of the problem than is possible here. See also reviews by Prenant ('10) and Eklöf ('14). In view of these very adequate discussions of the older literature, I have made rather sparing reference to the older workers in the present review.

There has recently developed in the place of the earlier functional interpretation of the chondriome in morphological terms, a tendency to interpret its rôle in secretion as in the nature of an indirect contribution to some more immediate center of secretory synthesis (Bowen, '26d; Jacobs, '28; Parat, '28). It is becoming increasingly clear that only through some such indirect and largely invisible cooperation with other parts of the cell can the chondriosomes share in secretory synthesis. This view is further suggested by their distribution among the secretory droplets and other facts of similar import. However, if such a cooperative effort on the part of the chondriosomes is actually included in the direct line of secretory formation, it must be confessed that we have at present no tangible picture of the process.

The central apparatus

Amid this veritable maze of conflicting observations, of which many must certainly be incorrect, it is a pleasure to record the fact that no one has succumbed to the temptation of including the central apparatus in the list of possible organs of secretory synthesis, although its possible relation to the discharge of secretory products has been the subject of some controversy (refer, for example, to Gurwitsch ('01)). Papers like that of Gurwitsch ('01) offer the nearest approach to any possibility of secretory activity. Clearly the central apparatus may be summarily dismissed as far as its participation in secretion is concerned.

The Golgi apparatus as the focus of secretory activity

> In erster Linie—und das ist das wesentlichste—treten die primären Granula als solche nur an den Maschen des Binnennetzes auf.
>
> Nassonov, 1923.

The possibility that the Golgi apparatus might be connected with secretion is not a recent idea but dates almost from the very beginning of serious study of this structure. Negri, indeed, in 1900 studied the Golgi apparatus in the pancreas-cell and differentiated it clearly from the intracellular secretory ('excretory') capillaries, a result later corroborated by Kolster ('13), and Sundwall ('16). His remarks on this point have often been taken to mean that he expressed an opinion on the relation of the Golgi material to secretory synthesis, but a careful reading of his paper offers no basis for such a statement. Subsequently v. Bergen ('04), Kolster ('13), and Cajal ('14) considered the possible relation of the Golgi apparatus to secretion, but concluded that any morphological changes in the apparatus which might be correlated with the secretory cycle, were merely passive results of the mechanical situation within the cell. Fuchs, on the other hand, in 1902 described a "Fadenknäuel" in the cells of the epididymis which he connected with the secretory process, observing that the first secretory granules appeared within it, but not by its direct transformation. He subsequently (1904) modified this interpretation in favor of a nuclear origin of secretion; and the connection of the thread-structure with secretion was also denied by Jeleniewski ('04). There is no doubt now that the structures which Fuchs ('04) described in the cytoplasm are the Golgi apparatus, although he himself denied their equivalence to the trophospongium, a structure, the relation of which to the Golgi apparatus was at that time much discussed. Indeed, the relation of the trophospongium of Holmgren to secretory synthesis never received any very definite expression. In any event, so far as the trophospongium is actually the Golgi apparatus of other authors, the vague statements of Holmgren can not be taken as an adequate forerunner of recent views of the rôle of the Golgi apparatus in secretion. The most nearly positive statements by Holmgren connecting the trophospongium with secretion seem to be contained in his remarks on the pancreas-cell ('02b). However, the nearest approach to the modern viewpoint was undoubtedly reached by Prenant ('05), who described in certain amphibian gland-cells what he termed an "amas vermiculaire," and associated with the ergastoplasm. The secretion is first deposited in contact with the substance of this vermicular mass and Prenant says in explanation, "Il y a donc bien certainement une relation topographique et peutêtre un rapport causal entre le protoplasma différencié de cette région cellulaire et le produit de sécrétion." If one substitutes 'Golgi apparatus' for 'vermicular mass' this account would be essentially up to date. Further review of the opinions formerly expressed will be found in Nassonov ('23, '24), and Kopsch ('26), who cite a number of references here omitted.

The recent development of the subject is, however, quite original and was first made possible by the development of methods of osmic impregnation which on one hand supply incomparable demonstrations of the Golgi material itself, and on the other hand permit a simultaneous and almost perfect demonstration of the secretory products. This result is attained by first fixing the material in a fluid which is known to give a reliable fixation image (e.g., Champy), and then blackening the Golgi apparatus by proper subsequent treatment with osmic acid. In this latter operation the delicacy of the original fixation is not particularly damaged, and in many cases the secretory granules can be rendered surprisingly visible by a final staining with acid fuchsin. Such preparations of vertebrate gland-cells were first achieved by Nassonov, whose initial contribution in 1923, foreshadowed by the studies of Deineka ('16), and Kolatchev ('16), very exactly marks the origin of recent views on the subject.

In approaching the problem of a possible causal relation between Golgi apparatus and secretory granules, certain definite facts concerning the topography and distribution of the Golgi material in glandular tissue should be clearly in mind. In a general way, and avoiding the still unsolved problems of its exact structure, the Golgi apparatus seems to consist of a substance of specific type, in which lipoidal material is a conspicuous factor. In animal cells, this material occurs in the cytoplasm of gland-cells in two morphologically different forms. In one case, the material forms a tangled meshwork or platework which is often rather compact and forms a unit structure (figs. 10, 11, 12, and 16). In the other case, the Golgi material is scattered in the form of discrete pieces or 'bodies' (figs. 14, 15 and 18). Between these two extreme types there are many intergrading conditions, and the compact type is in some kinds of gland-cells regularly fragmented into Golgi bodies at a more or less definite period in the secretory cycle (lipoidal gland-cells, for example, (fig. 18); cf. Bowen ('26b)). The point is, however, that the mere morphology of the Golgi apparatus is immaterial, it is the substance itself which is of consequence (Bowen, '26d). The reasons for its assumption of such protean forms are quite unknown, but this behavior is clearly not associated primarily with con-

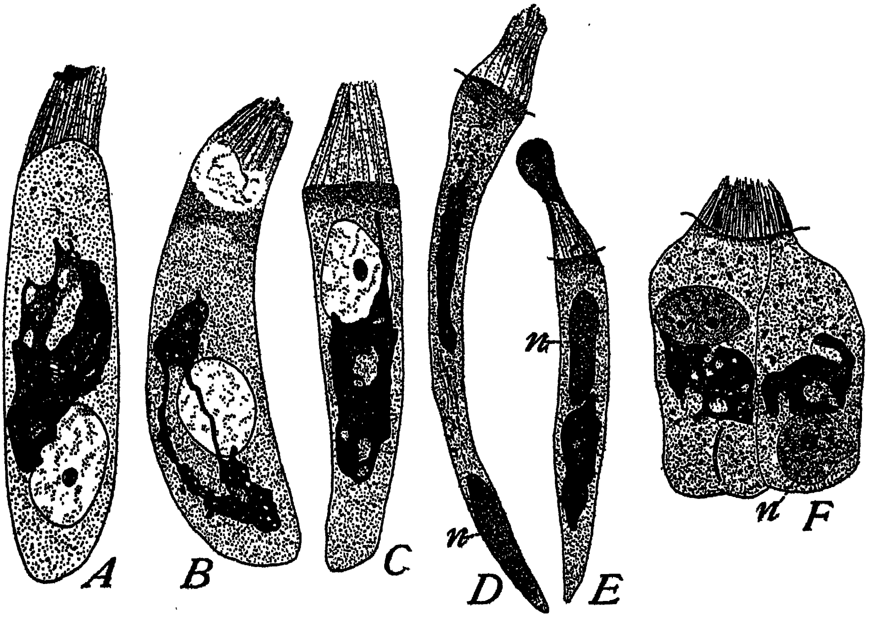

Fig. 10. Relation Between Secretory Polarity of a Gland-Cell and Position of the Golgi Apparatus; The Glandular Lumen Lies in Each Case at the Top of the Figure

A to *E*, from the cauda epididymis of the cat; *A* and *D*, normal polarity of the Golgi apparatus in 'active' and 'exhausted' cells respectively; *C* and *E*, reversed position of the Golgi apparatus in corresponding cells; *B*, intermediate position of the Golgi apparatus.—*F*, normal and reversed position of the Golgi apparatus in adjacent cells, from the vas deferens of the cat. *n*, nucleus. From Bowen, 1926.

ditions peculiar to gland-cells, since the same dispositions are met with in other types of somatic cells and in germinal tissue.

It is a general characteristic of the Golgi apparatus in gland-cells to present a rather marked polarization, in other words, to be concentrated in the zone between the nucleus (usually located in the basal region of a gland-cell) and that surface of the cell where the secretory products are characteristically extruded (figs. 10 and 11). Such a polarized condition was first emphasized by Cajal ('14) and Duesberg ('14), was also remarked on by Holmgren ('02b) in reference to his trophospongium, and is commonly found in many types of cells. In gland-cells the polarized position is regularly relinquished in certain kinds of glands (e.g., sebaceous (fig. 18), Bowen, '26b) in the later phases of the secretory cycle—a phenomenon which in many cases at least seems related to the fact that the entire cell is in these glands finally extruded. This whole matter will receive further consideration on a later page. The fact that the Golgi apparatus does present such a regular correlation with the place of origin and direction of discharge of the secretory products, has led Cowdry ('22) to suggest that the apparatus might be taken as an indicator of secretory polarity (compare also Courrier and Reiss ('22), Reiss ('22), Jasswoin ('24), Ludford and Cramer ('28)). This view was based upon the fact that in the thyroid gland of the guinea-pig, Cowdry found cases in which the apparatus was now on one side, now on the other, of the nucleus, and he interpreted this change in position as indicating the discharge of secretory material now into the cavity of an alveolus, now directly into the circulation. That the polarity of the Golgi material does coincide with the direction of the excretory current is in general certainly true, but it was pointed out by Bowen ('26c) that in a number of cases the polarity of the Golgi apparatus is reversed without any evidence of a corresponding change in the direction of excretion (fig 10). This matter has since been especially studied by Giroud ('26, '28) and Turchini ('27), and it now seems reasonably certain that the position of the Golgi apparatus is an uncertain guide, and is accordingly useless in exactly those doubtful cases in which we most need some readily identifiable clue to the direction of excretion. In this connection the observations of Nassonov ('27) on the mammalian epididymis are of unusual interest. In this case secretion-products of two different kinds are manufactured in the same cell, the direction of extrusion in one case being toward the glandular lumen, in the other toward the base of the cell. Compare also Nemiloff ('26).

Taking now a specific case to illustrate the general situation in a gland-cell, a good example is the pancreas of the axolotl as described by Nassonov ('23) in his first contribution. In these pancreas-cells the Golgi apparatus consists of a lamellar meshwork located in the typical position for a gland-cell (fig. 11). In the earlier phases of the cycle the secretory granules all lie within the general area enclosed by the Golgi network, where they are easily visible as yellowish spheres, or, after staining with acid fuchsin, as conspicuous red granules. In the majority of gland-cells in vertebrates, this area would obviously correspond to the region close to the nucleus and on the side toward the glandular lumen (fig. 10), and this region has often been noted as the place of first appearance of secretory droplets by workers most of whom had no intimation of the presence of the Golgi apparatus (cf. Leydig ('57), Bensley ('98), Maximow ('01), Schmincke ('03), Arnold ('05), Weiss ('09), Key ('16), Saguchi ('20a, the 'secretogenous area'), etc.) As the production of granules proceeds, the Golgi area, by which I mean merely to denote the space roughly included by the peripheral limits of the Golgi material, sometimes becomes gorged with secretion, like a basket filled with cherries (fig. 11*A*). Eventually the granules begin to move away and collect in the area of the cell next the glandular lumen (figs. 11*B* and *C*).

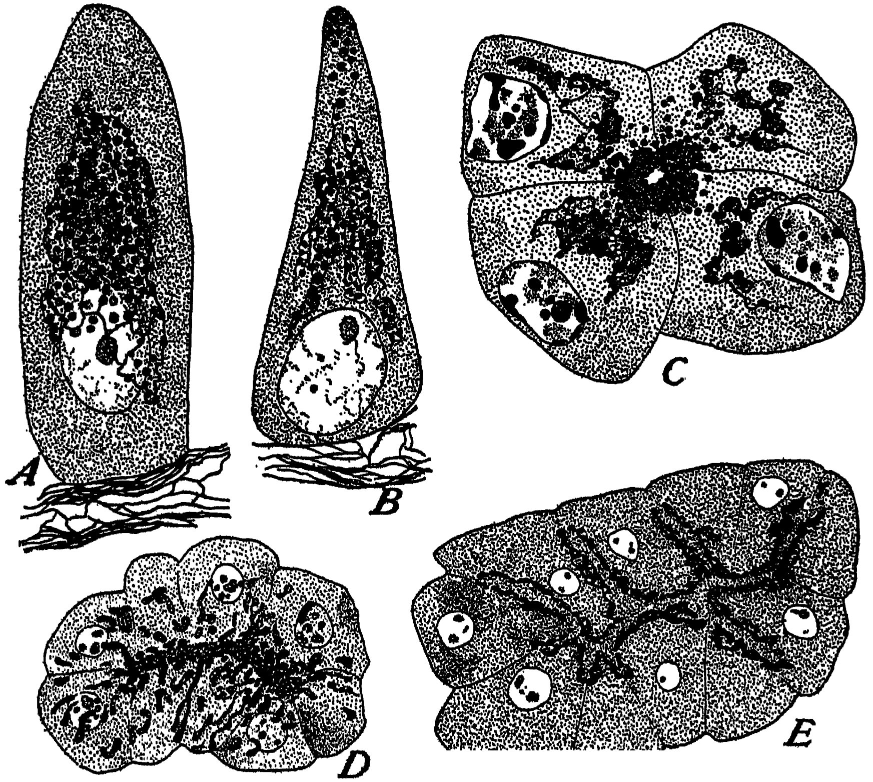

Fig. 11. The Golgi Apparatus in Relation to Secretory Activity in the Pancreas

A to *C*, from the axolotl; *D*, *E*, from the mouse, three hours after injection of pilocarpine—*D*, stained by the Kull method, to show the chondriosomes and the appearance of new, as yet very small, secretory granules along the border of the glandular lumen; *E*, similar cells prepared to show the Golgi apparatus, for comparison with *D*. From Nassonov, 1923 and 1924.

An equally good example, of a slightly different type, is the goblet cells of the intestine in Amphibia (Nassonov, '23; Bowen, '24a). Here the Golgi network is disposed like a long cylindrical meshwork in the area just distal to the nucleus (fig. 12). This becomes filled with secretory droplets which gradually migrate out to build up the familiar 'goblet,' and in the final stages the whole Golgi apparatus collapses (Bowen, '24a) as though to express the remaining secretory products, as the contents of the goblet are made ready for release. The fact is thus clearly established that an intimate topographical relationship exists between the Golgi material on one hand and secretory products on the other. The first step in the analysis of the situation thus presented is obviously to make an extended examination of glandular tissues to ascertain whether topographical relations of the same type everywhere obtain. If there is any causal relation between the Golgi material and the origin of secretion-droplets, one might then expect to find an intimate and invariable topographical relation. The facts have now been examined in a considerable variety of gland-cells, a partial tabulation being given by Jacobs ('27), and on the basis of this evidence Bowen ('26d) has pointed out that there are certain rather obvious differences in the topographical details, which may be shown often to correspond in a rough way with the type of gland-cell. The simplest arrangement is that which occurs in the goblet-cells, described above, and likewise in salivary glands of the mucous type (Bowen, '26a), lachrymal glands (Bowen, '26c), glands of the male reproductive tract (Bowen, '26c; Nassonov, '27; Parat, '28), etc. In these cases, the secretory droplets clearly have their origin within the Golgi area, but are rapidly completed and move away toward the glandular lumen to be stored until occasion arises for their extrusion (fig. 12). In some gland-cells of this type the stored products may apparently be extruded in part at least

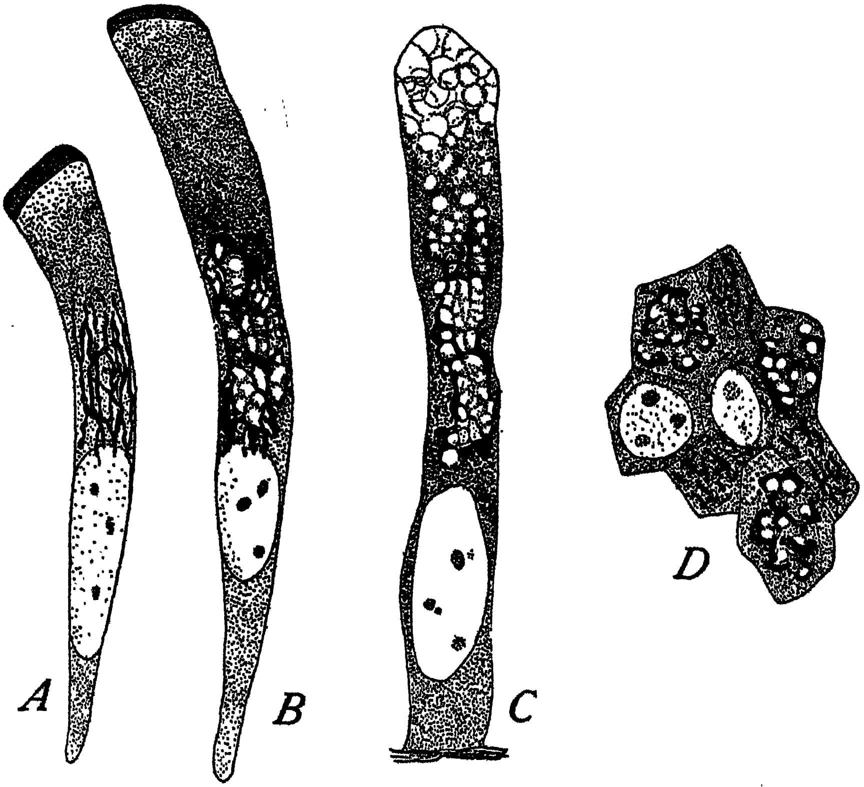

FIG. 12. THE GOLGI APPARATUS IN RELATION TO SECRETORY ACTIVITY IN CELLS OF THE INTESTINAL EPITHELIUM OF TRITON

A to *C*, steps in the formation of the characteristic 'goblet' at the free end of the cell; *D*, cross-section of cells in various phases of the secretory cycle. The secretory droplets appear as clear unstained vacuoles. From Nassonov, 1923.

without any essential disturbance of the active zone of secretory synthesis. Thus a continuous secretion-stream pours slowly out of the Golgi area, proceeding, after a longer or shorter pause, on out of the cell into the lumen of the gland.

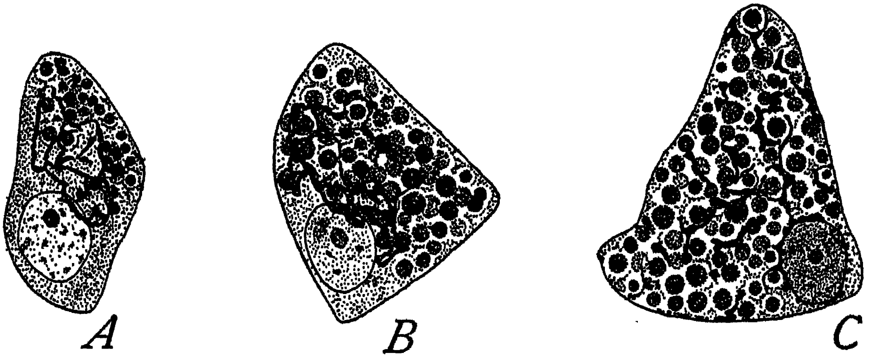

Fig. 13. The Golgi Apparatus in Relation to Secretory Activity in the Parotid Gland of the Cat, Showing the Progressive Extension of the Golgi Network Throughout the Mass of Secretory Droplets

From Bowen, 1926

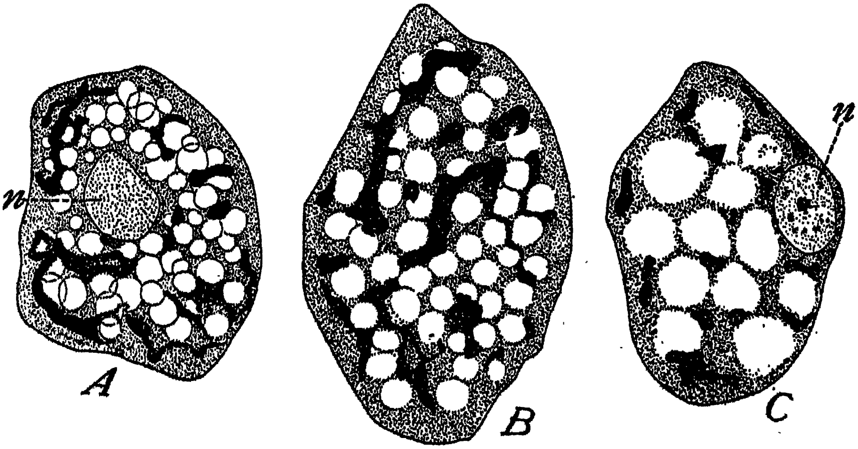

Fig. 14. Stages in the Secretion of Lipoidal Material in the White Portion of the Inguinal Gland of the Rabbit

A, *B*, earlier phases in the production of lipoidal droplets; *C*, later stage of fusion of droplets, with accompanying disintegration of the Golgi material. *n*, nucleus. From Bowen, 1926.

In other kinds of glands, however, the granules seem to require a longer period for their production, involving a process of 'maturing' which affects all of the secretory droplets simultaneously. This phenomenon was clearly described by Altmann ('94) in the parotid of the cat, and has since been noted by several other workers (e.g., Bowen, '26a). While there is reason to believe that the maturing of the granules may be quite independent of the Golgi apparatus, nevertheless the synthesis, by more or less simultaneous growth, of a whole batch of secretory granules, introduces a complicating factor. This situation seems to be met by the expedient of extending the Golgi material in all directions through the mass of secretory products, close topographical relations being thus retained throughout the period of development (fig. 13). Such is the condition in the parotid gland of the cat, where the apparatus gradually loses its initial, rather compact form, and insinuates itself in all directions among the developing granules (Bowen, '26a).

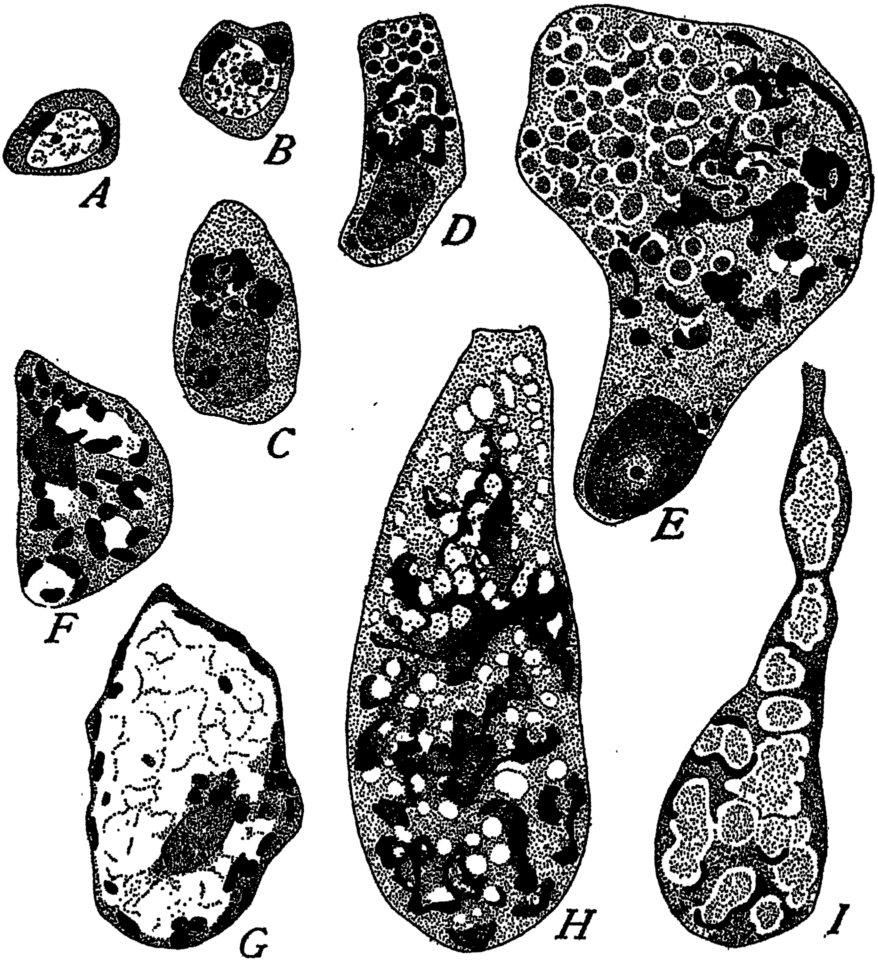

Fig. 15. Scattered Condition of the Golgi Apparatus—Golgi Bodies—Frequently Found in the Gland-Cells of Invertebrates

A to *E*, progressive stages in the secretory cycle of a serous cell from the salivary gland of *Limax; F, G*, earlier and later stages respectively of mucous cells from the salivary gland of *Limax;* from Bowen, 1926.—*H, I*, deep-lying mucous cells in *Hirudo;* from Nassonova, 1927.

The same end might, likewise, be accomplished by distributing the Golgi material throughout the mass in the form of scattered pieces. This is actually what happens in another group of cases, the result being attained in two slightly different ways. In one type, represented by the so-called 'skin-glands,' which produce lipoidal secretions, the apparatus is at first compact, but very early in the secretory cycle it begins to fragment, and the products, in larger (inguinal gland of the rabbit (Bowen, '26b), and mammary glands (Da Fano, '22); (fig. 14)), or smaller (avian oil glands, Meibomian, sebaceous, and Harderian glands (Bowen, '26b; Ludford, 25), (fig. 18)) pieces become scattered more or less throughout the secretory mass, depending on the method of extrusion which happens to obtain in the particular case. In another type, common in invertebrate gland-cells, the apparatus is from the first in the form of discrete Golgi bodies which become widely scattered among the developing secretory granules (fig. 15). In some of these cases more or less fusion of the droplets is known to occur in the later stages, and this suggests that a similar process might be one way in which large granules could be produced at points removed from direct topographical relations with the Golgi apparatus.

One further type of association between secretory granules and the Golgi material remains to be mentioned, although in my own opinion the validity of the interpretation is not yet above suspicion. The situation occurs in some gland-cells in which the granules grow or undergo marked changes after leaving the Golgi area. The individual granules in these cases seem to carry away a small portion of Golgi material in the form of a 'girdle' or 'cap' (Nassonov, '23; Bowen, '24a), which might be regarded in much the same light as the case of the scattered Golgi bodies previously described (fig. 16). Unfortunately, the occurrence of somewhat similar structural peculiarities in cases where the presence of Golgi material would appear not to be a satisfactory explanation, suggests that a final conclusion be deferred until a more extended and critical examination of this situation can be made.

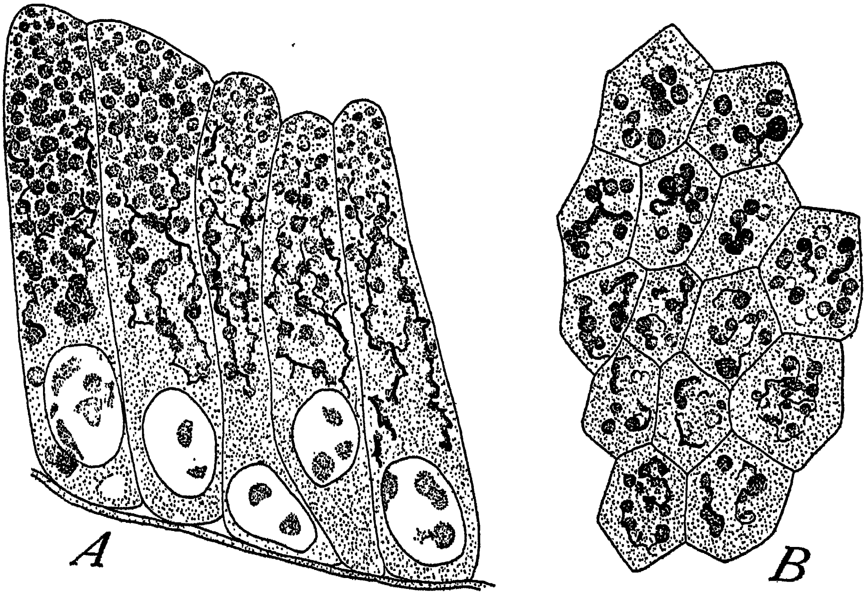

FIG. 16. LONGITUDINAL AND CROSS-SECTIONS OF CELLS FROM THE PELVIC GLAND OF TRITON, SHOWING RELATION OF THE SECRETORY DROPLETS TO THE GOLGI NETWORK AND TO THE OSMIOPHILIC GIRDLES
From Nassonov, 1923

If one now considers the general types of behavior presented by the Golgi apparatus in gland-cells of different kinds, he will be struck by an obvious, if rough, correlation with the old histological classification of glands. Thus, Bowen ('26d) has pointed out that in gland-cells of the 'mucous type,' the apparatus tends to maintain a rather fixed relation to the zone of developing granules, the granules themselves moving quickly away as rapidly as they are formed—as in the case of the goblet-cell. In some glands of the 'serous type' where a period of maturing may occur, the Golgi material spreads throughout the mass of developing granules, as in the parotid of the cat; while glands of lipoidal secretion are marked by the fragmentation of the Golgi material and its distribution throughout the secretory product. One might indeed classify many glands from a knowledge of the behavior of their Golgi apparatus, in the absence of any other information as to their nature, as in the case of the crescent-cells of Gianuzzi in the submaxillary of the cat, described by Bowen ('26a).

Before concluding this discussion of the purely topographical features of the Golgi apparatus in gland-cells, there are several associated points which should be emphasized.

In the first place, it is important to note that during the secretory cycle the Golgi apparatus undergoes a marked hypertrophy. This was first pointed out clearly by Cajal ('14), who came very close to the view of the Golgi apparatus which was later suggested by Nassonov. It is, however, to be particularly noticed that this increase in the amount of Golgi material is related to the volume of the secretion-product rather than the undifferentiated cytoplasmic background or the nucleus—both of which may appear actually to decrease in size as the secretory cycle progresses. When it is further considered that the chondriosomes have been said by some (page 489) to decrease during secretion, the significance of the hypertrophied Golgi material may be more apparent. If it is reasonable to suppose that the elements involved in secretory activity would show changes in the direction of increased activity as expressed in size-increase and change in morphology, then it seems significant that the Golgi apparatus shows exactly such changes, while the other elements of the cell appear to fall more and more into the background as the secretory cycle draws on toward its conclusion (cf. Bowen ('26d)).

In the second place, it is indirectly significant that the Golgi material itself is not visibly used up during secretory activity, in other words that it does not itself seem to be transformed into the secretory granules. Practically all workers agree on this point, although Jacobs ('28) comes to a contrary conclusion in the case of certain intestinal gland-cells in *Astacus* (see also Nemiloff('26)). Nevertheless, it is clear that Golgi material is in some cases extruded with the secretory product proper. This is obvious in the case of glands of the holocrine type (the inguinal gland of the rabbit is a good example, Bowen, '26b), and may very likely occur to some extent in any gland-cell from which there is a very extensive excretion at any one time. It is also worthy of note, that Golgi pieces can sometimes be demonstrated among the extruded secretion-products (fig. 17), thus indicating that it possesses a distinct, material reality which is retained even after leaving its normal cellular location (cf. Brambell ('25), Bowen ('26b), Beams ('27)). Brambell ('25) believes that in the secretory cells in the oviduct of the hen, the Golgi material is entirely cast out of the cell together with the secretion proper, to be reconstituted de novo for the next secretory cycle. Other workers who have particularly examined early phases in the secretory cycle, of which the pancreas-cell in the mouse as described by Nassonov ('24) offers an especially good example (fig. 11 *E*), have, however, failed to corroborate this account. It seems certain, therefore, that merocrine gland-cells usually retain part of the Golgi material, which, after sharing in the necessary reorganization which may mark the close of a secretory cycle, is retained as the definitive Golgi material.

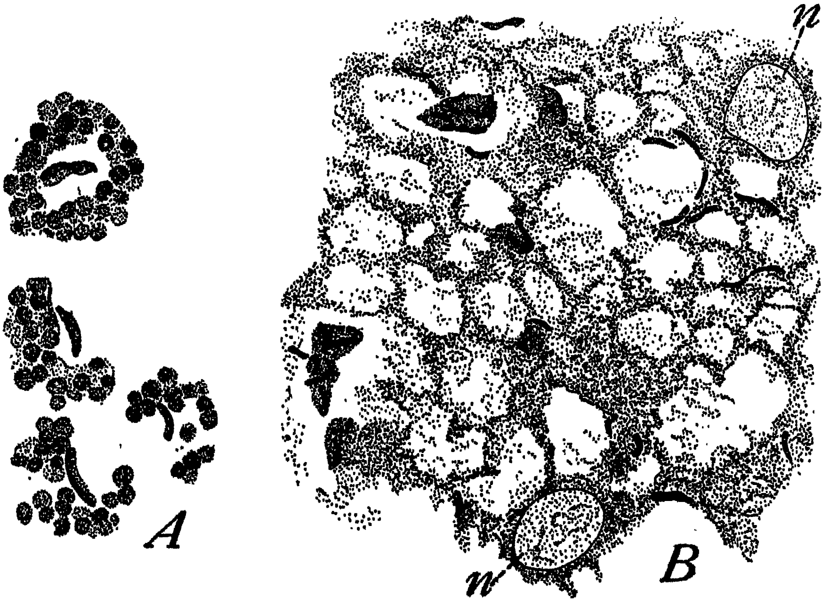

FIG. 17. MAINTENANCE OF THE CHARACTERISTIC FORM OF THE GOLGI APPARATUS (GOLGI BODIES) AFTER BREAKDOWN OF THE CELLS IN WHICH THE APPARATUS WAS ORIGINALLY CONTAINED

A, secretory granules and Golgi bodies from the oil-gland of the duck; *B*, secretory mass with contained Golgi bodies after disintegration of the cells in the red portion of the Harderian gland of the rabbit. *n*, nucleus. From Bowen, 1926.

It is thus evident that in a very long series of gland-cells, in both vertebrates and invertebrates, the fact has been established that there is a constant topographical relation between Golgi apparatus and secretion-products in process of formation, the Golgi area marking, indeed, the invariable focus where secretory droplets make their initial appearance. This topographical interrelation has been dealt with by Nassonov ('23, '24, '26, '27), Bowen ('24a, '26a, b, c, d), Jasswoin ('25), Kopsch ('25, '26), Ludford ('25a, b), Cramer and Ludford ('26a, b), von Lanz ('26), Nemiloff ('26), Beams ('27), Morelle ('27a), Nassonova ('27), Tschassownikow ('27), Urasov ('27), Ludford and Cramer ('28), and Parat ('28); reference should also be made to Cramer and Ludford ('25), and Weiner ('28) on fat-absorption in the intestinal cells. A general discussion of the topographical situation is given by Nath ('26) and Jacobs ('27). Not only is there a mere spatial relation between secretory products and Golgi material, but the latter has been shown to assume various types of arrangement correlated with the kind of secretion that is being synthesized. Of all the cellular constituents, it is the Golgi apparatus alone which seems to present morphological features peculiarly connected with secretory phenomena within the cell. Such a close spatial interrelation is a prime necessity of Nassonov's theory, and it is worthy of peculiar emphasis that no one has yet found a case where these topographical considerations could be denied, except perhaps in certain cases described by Chlopin ('27), the exact relation of which to the Golgi apparatus is problematical, and Beams and Wu ('29) on insect spinning glands.

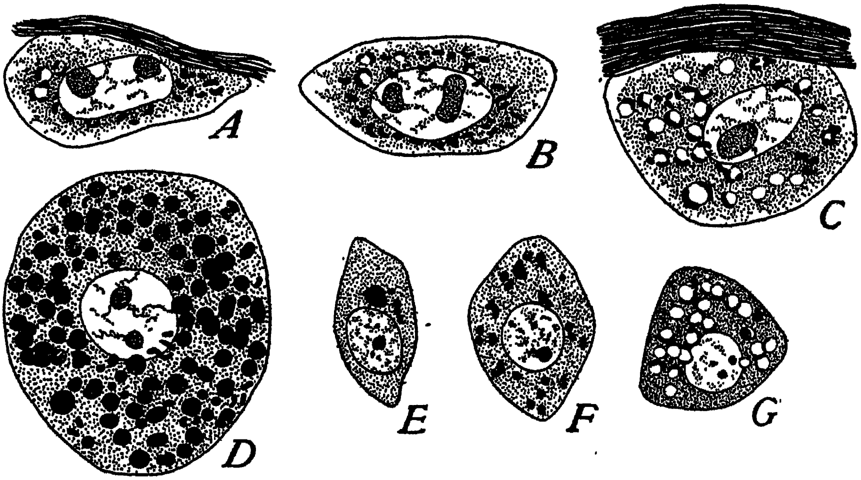

Fig. 18. Relation of the Scattered Golgi Bodies in Some Glands of Lipoidal Secretion to the Individual Secretory Droplets

A to *D*, progressive stages in sebaceous glands of the mouse. From Ludford, 1925.—*E*, earliest, condensed condition, and *F*, later scattered condition of the Golgi apparatus in the oil-gland of the common fowl; *G*, later phase of the same, showing intermediate stage in the production of fatty droplets. From Bowen, 1926.

The general topographical interdependence of Golgi apparatus and secretory granules having been thus established with reasonable certainty, the problem remains as to the more exact relation of individual secretory granules to the Golgi material. In exactly what terms can we picture this relation from a standpoint not only morphological but physiological as well. Certain aspects of this problem are as yet entirely obscure, owing to the fact that the intimate structure of the Golgi material is still relatively little understood. Indeed, recent comment on this particular phase of the Golgi-problem has served only to increase rather than decrease the difficulties of interpretation (e.g., Bowen ('24a, '26b, '27), Hirschler ('27), Parat ('28), and Morelle ('27a and b)). From a morphological point of view the appearances suggest that the secretory vacuoles arise de novo within, or on the surface of, the Golgi material, and remain in close physical relation with the Golgi apparatus during their development. Unfortunately, in practically all cases, the number of secretory granules present in a single cell is so great, and the exact limits of the Golgi apparatus so ill-defined, that a clear-cut picture of the exact nature of the relation is difficult to obtain. The figures of the amphibian goblet-cell given by Nassonov ('23) are perhaps as suggestively clear as any (fig. 12). There is, however, one case in which the topographical relationship seems remarkably definite. This is in certain gland-cells producing lipoidal secretions. Ludford ('25b) in sebaceous glands of the mouse and Bowen ('26b) in the oil gland of the fowl, independently observed that the fragments of the Golgi apparatus, characteristically formed in such glands, are associated with specific, individual, secretory droplets (fig. 18). In such a case, each granule seems to be associated with a small piece of Golgi material, and the topographical situation is reduced to its ultimate terms. Unfortunately, in both of these accounts, the whole story was not made out. The material is, further, technically difficult, and the case offers some other features which might justify another interpretation in the absence of a complete account of the Golgi material in absolutely every phase of the secretory cycle. It seems to me, therefore, the part of wisdom to defer final acceptance of the validity of these descriptions pending more adequate examination. Nevertheless, the possibilities suggested are of critical importance and offer the best present chance of a crucial proof of Nassonov's theory.

With respect to the ultimate origin of the secretory droplets, however, there are other conceivable possibilities, as Nassonov ('23) suggested in his first contribution. For example, the original granules might be derived from the fragmentation-products of mitochondria or from some ultimate protoplasmic particles like Heidenhain's 'protomeres.' Nassonov himself has never attempted to develop these suggestions into the status of probabilities, and the great majority of workers have not found any evidence to support the view that the beginnings of secretory granules are found in chondriosomes or other definite particles of the cytoplasm. However, certain workers (see page 321), have considered mitochondria as the source from which comes the material worked upon by the Golgi apparatus. But I think it fair to conclude that the weight of evidence is in favor of viewing the earliest secretory vacuoles as structures not to be traced to any direct morphological relation with cellular structures previously present in the cell.

The very recent work of Benoit ('26), Hirschler and Hirschlerowa ('28), and Parat ('28) and his colleagues has thrown a great deal of light upon this whole problem of secretory beginnings. The difficulty of studying the relation of the individual secretory droplet to the Golgi substance is due to the fact that the very earliest and smallest secretory droplets are not well demonstrated by the usual technical methods. Parat has shown, however, that exactly these stages in secretory synthesis can be stained by the intra-vital application of neutral red. The very smallest droplets or vacuoles are thus brought clearly to view, and the whole story of their transformation into secretory droplets can be traced. It is clear that the vacuoles arise in the Golgi area, probably through its activity, and thus is furnished a constant source of new secretory vacuoles. These earliest phases of secretory synthesis constitute the "vacuome" of Parat. Within each vacuole appears the segregation granule (of Renaut, p. 307), which itself is not usually stainable by neutral red but can be demonstrated after fixation, by acid fuchsin. As the secretory droplet grows to maturity, its capacity for staining with neutral red disappears coincidently with the filling up of the enclosing vacuole. As Benoit ('26) has clearly pointed out, although Parat ('28) himself offers a rather different interpretation, (see page 507), the topographical relation of the vacuome,—i.e., the primordial secretory droplets,—and the Golgi apparatus leads to the conclusion that the vacuoles originally appear embedded in or on the Golgi material, and subsequently become free as recognizable secretory droplets (fig. 19*A*). And this conclusion is supported by many of the results of osmic impregnation, in which the vacuolated appearances of the Golgi material were for some time a source of difficulty (e.g., Bowen, '26c).

The problem remains as to the nature of the physiological relation possibly existing between the Golgi material on one hand and the contents of a secretory vacuole on the other. There is obviously no direct evidence as yet which bears on this point, but two possibilities are more or less implicit in published work. Of these, Nassonov ('26) in particular regards the Golgi apparatus as active only in the elective concentration of the secretory materials, which are themselves primarily the product of chemical synthesis in the general protoplasm. The other view, which I have myself held in rather indefinite form, considers the Golgi apparatus as taking some active part in the synthesis of the final secretion-product. The evidence now at hand can scarcely be said to warrant any particularly decided opinions on the point in question.

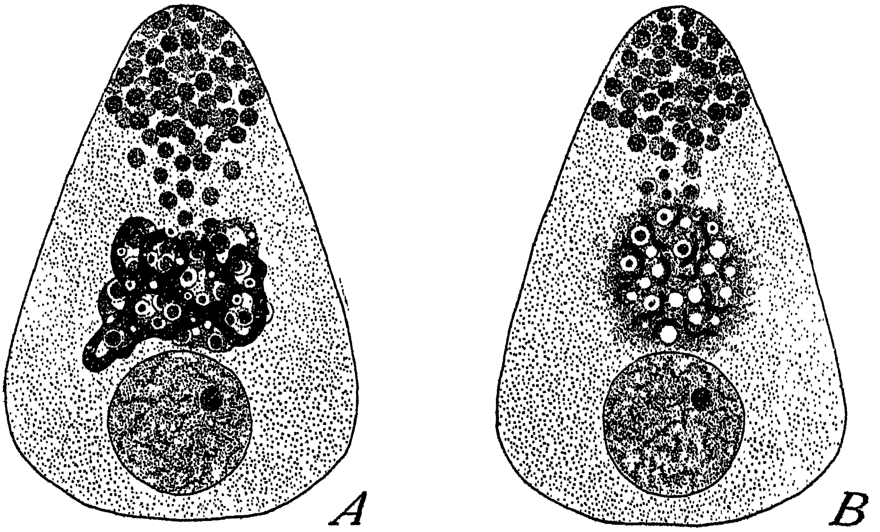

FIG. 19. SCHEMATIZED REPRESENTATION OF THE TWO VIEWS OF THE ARCHITECTURE OF THE SECRETOGENOUS AREA IN A GLAND-CELL

A, the Golgi apparatus and its relation to the secretory droplets, according to Bowen and others. *B*, the secretory droplets (in their earlier phases, the vacuome) and their relation to the "diffuse lipoids" (more heavily stippled area) and "active chondriome" (black, rod-like bodies in the area of diffuse lipoids) of the secretogenous area, according to Parat, 1928.

There is, however, another source of extraordinarily interesting data bearing on the problem both morphologically and physiologically—namely, the relation between the Golgi apparatus and the secretion of so-called vital dyes. As is well known from the researches of Möllendorff, vital dyes behave toward protoplasm in two quite different ways according as the dye is acid or basic. Basic dyes enter cells without difficulty and are deposited in (in other words, stain) bodies such as chondriosomes (in the case of janus green) or vacuoles (in the case of neutral red), which had a perfectly definite preexistence in the cell. Acid dyes, on the contrary, enter relatively few kinds of cells, which must in addition be in their proper place in the living body. But in such cases, the dye is deposited not in preformed elements of the cytoplasm, but in new formations (vacuoles) which are part and parcel of the reaction of the cell to the dye. In other words, acid dyes are 'secreted' within the cell in a manner which, morphologically at least, recalls some of the characteristic features of normal secretory phenomena. If the production of a secretory granule is thus in a sense comparable to the formation of a granule of a soluble vital dye, one may suppose that the action of the cellular mechanism is in the two cases similar in at least some respects. We should expect, therefore, under these possible circumstances, to find that the secreted granules of vital dyes bear the same topographical relations to the Golgi apparatus as the true secretory granules.

The possibilities of such histophysiological examination have now been rather adequately investigated, and the actual results have borne out in a most amazing manner the theoretical expectation. The first results were published by Jasswoin ('25) on the kidney-cells of Amphibia. These were soon amplified by Nassonov ('26) on the kidney of the axolotl, the white mouse, and the cat, the liver of the mouse and of *Lacerta*, and in a subsequent paper ('27), the epididymis of the rabbit and guinea-pig. Similar contributions have been made by Makarov ('26), Glasunow ('28), and Ludford ('28); and the suggestive experiments of Chlopin ('27) with neutral red, in the production of his so-called 'Krinome,' and the recent study of Rumjantzew ('28), should also be mentioned. All of the workers who have experimented with trypan blue concur in the conclusion that the distribution of the first-formed granules of the dye corre-

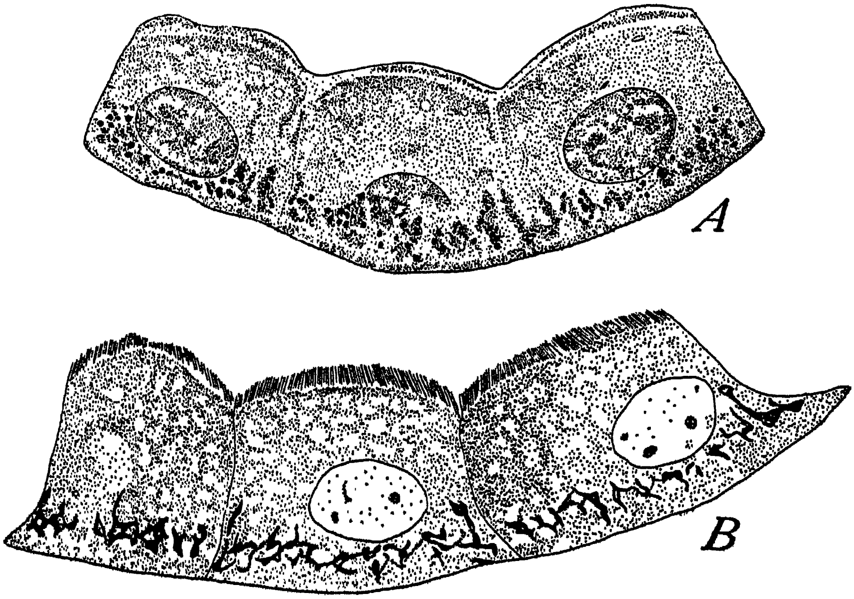

FIG. 20. RELATION OF THE GOLGI APPARATUS TO THE ACCUMULATION (SECRETION) OF A VITAL DYE (TRYPAN BLUE) IN THE KIDNEY-CELLS OF TRITON

A, the distribution of the vital dye; *B*, complementary preparation to show the corresponding topography of the Golgi apparatus. From Jasswoin, 1925.

sponds exactly with that of the Golgi apparatus. These results should be compared with Peter ('24) and with many of Möllendorff's figures, and also with the old observations of Krause ('01) and others of similar nature, which quite unknowingly demonstrated the topographical superposition of the granules of 'secreted' vital dyes on the Golgi apparatus. Thus in the kidney of *Triton* in certain cells Jasswoin showed that the Golgi apparatus had a rather striking distribution—basal to the nucleus (fig. 20 *B*). Similar animals are now given injections of trypan blue, and upon examination of the kidneys, cells are found with granules of the dye distributed in a corresponding way (fig. 20 *A*). Perhaps the most striking case of all is that furnished by the liver of *Lacerta* (Nassonov, '26), where the Golgi apparatus has a very unusual distribution adjacent to the bile capillaries (fig. 21*B*).

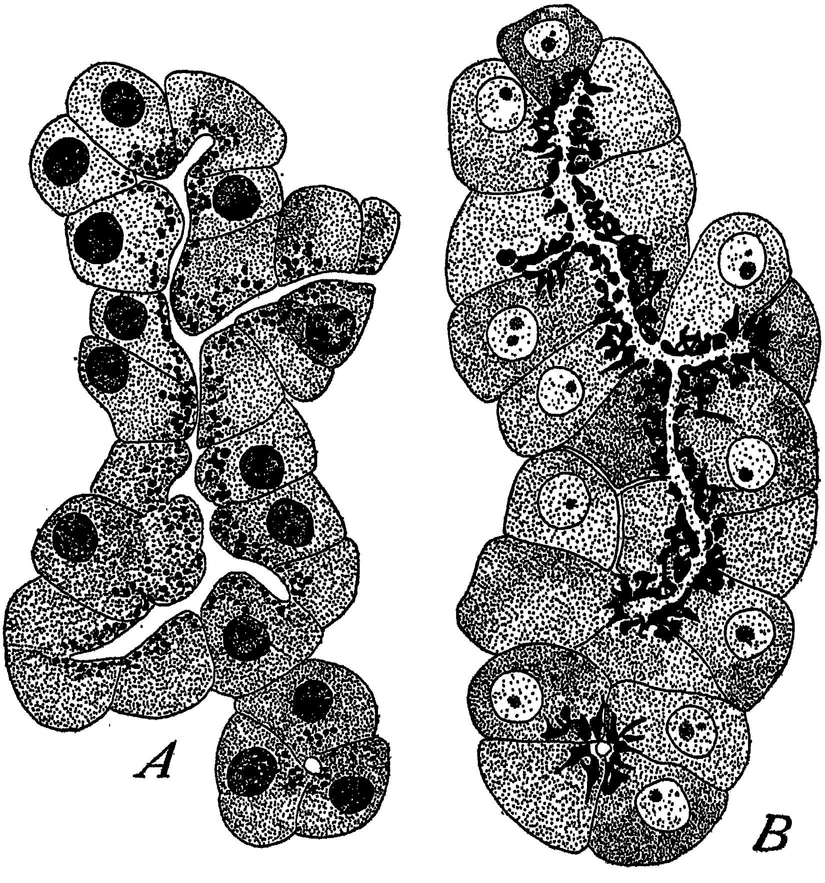

Fig. 21. Relation of the Golgi Apparatus to the Secretion of a Vital Dye (Trypan Blue), in Liver-Cells of Lacerta

A, *B*, like fig. 20. From Nassonov, 1926

Trypan blue injections result in the appearance of blue granules in the same position in the cell (fig. 21*A*). It is thus demonstrated beyond doubt that the cellular zone in which acid dyes are 'secreted' corresponds to the Golgi area, and that the dye-granules are never seen in any other part of the cell during the earlier phases of their production. Nassonov and Jasswoin were unable to impregnate the Golgi apparatus and still retain the natural coloring in the granules of vital dye. Their demonstration, while convincing, was thus lacking in one point which is of particular interest in view of the recent assertions of Parat ('28) as to the homology of vacuoles and the classical Golgi apparatus. This missing link has now been supplied by Ludford ('28), who has succeeded in blackening the Golgi material simultaneously with a staining of the granules of vital dye, the whole providing a remarkably conclusive demonstration of Nassonov's theory.

Thus the problem stands at the present moment. It is perhaps unnecessary yet to commit one's self finally to the view that in the activity of the Golgi apparatus is to be found the long-sought cytological explanation of secretory origins; but it is nevertheless proper to point out in no mistakable terms that Nassonov's account is the only view of the matter thus far expressed which has seemed to have any appearance of that universal applicability which any solution of the cytological problem of secretion must indubitably possess. Not only with respect to the purely morphological features, but in such physiological experiments as have thus far been possible, the fragments of evidence seem to fit logically into a single unified conception of the cytology of glandular secretion.

But, as I have elsewhere remarked, it is one thing to note certain obvious relations existing in a general way between the Golgi apparatus and a mass of secretory granules and to conclude therefrom that the Golgi apparatus produces the granules; it is quite another thing to reduce this relation to the critical case of a single granule and thus to arrive at some real conception of how secretory products are actually related to the Golgi substance. It remains now to inquire whether there is any further light to be thrown on this difficult point from some hitherto unsuspected angle.

It will, I think, be evident that the matter in question, like the whole problem of secretory origins, is made difficult primarily by the fact that secretory granules are present in a given cell in such large numbers that it is impossible to study any single or particular one in any detail. If we could find a secretory product of some kind which was produced as a single granule, or at most a very few granules, we could obviously study the phenomena of both origin and growth in a manner quite impossible in an ordinary gland-cell. It was pointed out by Bowen in 1923 (and more fully developed in later papers, '24a, and '26d) that exactly this kind of secretory product is already well known and has been very thoroughly studied as the so-called acrosome of the animal sperm. This structure has, to be sure, long been considered as a 'cutting-tool' modeled during sperm-formation out of almost any material that happened to be handy. But in a series of papers Bowen ('22, '24b, '25, etc.) has shown that this hap-hazard derivation of the acrosome is entirely a product of inadequate technique and inaccurate observation. The acrosome actually is a substance which is produced invariably in association with the Golgi apparatus of the spermatid. To put a long story into a few words, it is now perfectly clear that the acrosome is somehow a product of the activity of the Golgi apparatus, but that in its production the substance of the Golgi apparatus is not directly transformed into acrosomal material. When the acrosomal material has been produced, the Golgi apparatus is still present substantially as at the beginning of the process and is finally (in most cases) cast out of the sperm, like a useless remnant, together with other detritus of spermatogenesis. These waste materials together constitute the protoplasmic balls, the casting off of which from the nearly completed sperms is a process at once well known and characteristic. This history is in essence the cytological story of the production of a secretion-product, and the only question which can well be entertained about it, is whether this secretion, the acrosome, can be in any way compared with a glandular secretion, the zymogen granules, for example. Bowen believes that the evidence points unmistakably to the essential similarity of the acrosome with an ordinary secretion-granule. Not only does the acrosome present the same topographical relations to the Golgi apparatus, but morphologically it often presents the differentiation into a vacuole and an enclosed granule which is so obvious a characteristic of many secretory droplets (figs. 1 and 22 *B*). Thus Bowen suggests that from the standpoint of acrosome-formation, light is shed upon the details of the mode of origin and growth of secretory droplets, and that from the standpoint of the gland-cell, light is shed upon the real significance and function of the acrosome. He concludes therefore, with the suggestion that the acrosome is a secretory product pure and simple, the function of which is to set off the fertilization-reaction. Fuller statements of the views here outlined together with actual details of acrosomal behavior, will be found in Bowen ('22a, b, '26d, etc.).

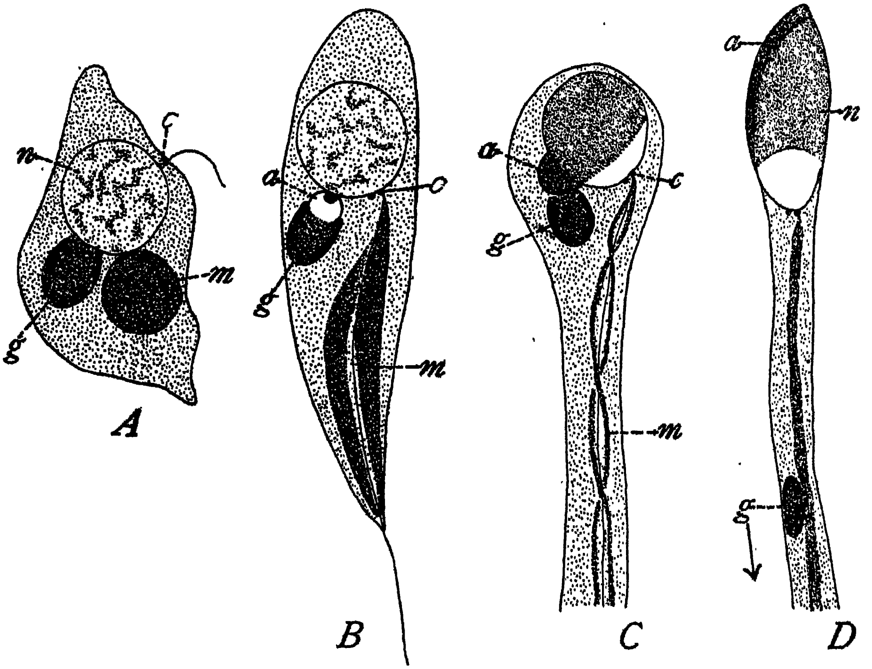

Fig. 22. The Relation of the Golgi Apparatus to the Formation of the Acrosome in the Animal-Sperm; Schematized Figures Based on the Conditions in Hemiptera, According to Bowen

A, early spermatid prior to the appearance of any acrosomal material; *B*, formation of the acrosome; *C*, separation of the Golgi apparatus from the acrosome; *D*, application of the acrosome to the developing sperm-head (nucleus) and retreat of the Golgi apparatus down the tail of the sperm. *a*, acrosome; *c*, centrioles and related axial filament; *g*, Golgi apparatus; *m*, chondriosomal body or nebenkern; *n*, nucleus.

The morphology of acrosome-formation becomes thus unexpectedly of prime importance to a more detailed understanding of secretory synthesis. The production of acrosomal material is subject to many variations in detail, but the essential points are well illustrated by Hemiptera of the family Pentatomidae. In these forms (Bowen, '22a), the earliest spermatid contains a number of scattered Golgi bodies which, by successive fusions, finally combine to form a single, thimble-shaped mass (fig. 22 *A*). The 'opening' of the thimble is turned toward, and is in contact with, the nuclear membrane. Presently there appears at the mouth of this thimble a small, clear vacuole (fig. 22 *B*), which gradually grows larger as the earlier phases in the transformation of the spermatid are progressing. Within this vesicle a characteristic granule (segregation granule?) presently appears. When this complex of vacuole and granule has been completed, the Golgi apparatus breaks away (fig. 22 *C*) and travels backward along the sperm tail—an apparently useless remnant (fig. 22 *D*). The acrosomal material, on the other hand, migrates around the nucleus and presently begins the series of morphological changes which finally result in the acrosome of the mature sperm (fig. 22 *D*).

We have thus, in the production of the acrosome, a large-scale simulacrum of the production of each secretory granule in a gland-cell, and the probable morphological relationship of Golgi material to secretory product is made transparently clear. Bowen himself did not extend his observations to living cells, but this final step in the evidence which would link together the acrosome and secretory granules as essentially expressions of a single phenomenon (secretion) has been recently completed by Parat ('28) and particularly by Hirschler and his pupils, and Gatenby ('29). Parat's work was partly done in collaboration with several of his students, and a bibliography will be found in the reference cited; of the papers from Hirschler's laboratory note particularly Hirschler ('28), Hirschler and Monné ('28). These workers have shown that in many cases the developing acrosome, sometimes the proacrosomal material also, responds to neutral-red staining in much the same way as true secretory vacuoles.

Concerning the physiology of acrosome-formation we know nothing as yet, but it is perhaps worth while to observe that the condition of the spermatid-chondriosomes, condensed as they are into the compact 'nebenkern,' permits a conclusive demonstration of the fact that the chondriome does not share in any direct (morphological) way in the synthesis of the acrosome (fig. 22 *B*), as the theory of Saguchi, Morelle, and others (see page 490) would seem to require. With respect to the physiological interpretation of the acrosome, and its function in the egg, as suggested by Bowen's hypothesis, it is interesting to note that Hibbard ('27) has recently brought forward evidence of the presence of an enzyme in the acrosome of the *Discoglossus*-sperm. This is the first positive indication that the interpretation of the acrosome as a secretion is correct. The older experiments of Goodrich ('20) on the behavior of the *Nereis*-egg from which the sperm had been removed by micromethods as soon as was possible after it (the acrosome?) had touched the egg, should also be taken into consideration here. This aspect of the situation is more fully discussed by Bowen ('25).

Whatever, therefore, the final judgment on Nassonov's theory may prove to be, it is even now impossible to avoid the conclusion that in some cases at least the Golgi apparatus is directly concerned in the production of secretions. Not least important in this conclusion is the fact that for the first time we have a conception of the secretory process which brings under one common viewpoint a series of hitherto unrelated phenomena—phenomena, indeed, whose possible relations to each other were not even suspected. Exactly how the Golgi apparatus operates we do not know, except that there is reason to believe that it does not function as an independent cell-organ. Secretory activity seems rather to be a function in which the whole cell-system is somehow involved, presumably in the sense that it cooperates in providing the raw or finished materials which are to be deposited in the secretory vacuoles. This point has recently been again emphasized by Jacobs ('28) (see also Ludford ('25a), Bowen ('26d), Tschassownikow ('27), Ma ('28a), Parat ('28)). In such a scheme of things, the nucleus and chondriosomes may well have some definite share and to this fact perhaps are traceable the changes which these cell-elements sometimes exhibit during the secretory cycle. But the center for the actual differentiation of visible secretions is the Golgi apparatus. The immediate source of secretory synthesis lies in the area presided over by the Golgi apparatus, and in that sense the Golgi apparatus may be said literally to produce the secretory droplets. Of many workers on the Golgi apparatus in gland-cells only Benoit ('26) (in certain cases), Parat ('28) (in certain respects) and Beams and Wu ('29) find this conclusion untenable, although a few, like Kopsch ('25, '26) and Urasov ('28), find the evidence still inconclusive.

The vacuome theory

In bringing this review to a conclusion, special mention should be made of a very recent view of the Golgi apparatus incorporated in the so-called vacuome theory of Parat, his recent summary (1928) of which gives complete bibliographical references and some rather important modifications of, and additions to the ideas which he expressed in his earlier, brief reports. With this theory we may also connect the views of Corti ('24, etc.) on his so-called 'lacunome.' According to Parat, the classical Golgi apparatus is largely mythical. He holds that the structures so classified really are of several unrelated kinds, such as vacuoles, "active" chondriosomes, diffuse lipoids, etc. Restricting the discussion to gland-cells in vertebrates, however, it is clear that his view of the secretory vacuoles, their morphology and place of appearance, is essentially that already outlined under the Golgi theory. But Parat finds in the Golgi area of other workers, not the classical Golgi apparatus, but a region of "diffuse lipoids" and "active" chondriosomes, in which the primordial secretory vacuoles (vacuome) are distributed. Evidently, the conditions in a gland-cell according to Parat, involve certain ideas which diverge rather sharply from the usual descriptions of the Golgi-area. Nevertheless, Parat's most recent development of the situation *in gland-cells* suggests differences from Nassonov's views which are more in the nature of interpretation than of fact. It would appear from the work of Benoit ('26) and Hirschler and Hirschlerowa ('28) that Parat's "diffuse" lipoidal area is merely another name for what others have called the Golgi apparatus. The primary matter in dispute turns then only on the question of whether this lipoidal material is in a "diffuse" (Parat) or formed (Golgi apparatus) condition (compare also Benoit ('26), Morelle ('27b)). Parat's insistence that the vacuoles (vacuome) are the structures which his predecessors have called the Golgi apparatus seems to me quite without warrant in fact, and is certainly and conclusively untrue in case of the male germ-cells, where the vacuoles in some cases are the acrosomal material and have never been confused with the Golgi apparatus.

Parat's conception of what he terms the "Golgi zone" in a gland-cell is shown in fig. 19 *B*. It will be observed to differ from fig. 19 *A* chiefly in the importance ascribed to the chondriosomes (his so-called "active" chondriome) in the Golgi area. This conception of "active" condriosomes is entirely new in animal cytology and has been frankly borrowed from Guilliermond's interpretation of the plant chondriome. There is little in the literature at present upon which this conception can find any secure footing, although a certain degree of support is furnished by the observations of Saguchi ('20a), Lewis and Maurer ('20), Urasov ('27, '28), Morelle ('27a), and Tschassownikow ('27). It will be further noted that Parat conceives of the vacuome as the all-important element in the organization of the Golgi zone, while Benoit ('26), Morelle ('27b), and others would view the vacuoles rather as the result of the functioning of the Golgi apparatus. Parat's whole interpretation of the cytoplasm is just now the subject of an acute and universal controversy, and it seems useless to attempt at present any further analysis of his views. But it will be evident that however this controversy may end, the outcome will leave Nassonov's hypothesis in the position of embodying many of the more important morphological features of secretory synthesis.

CONCLUSION

As one regards in retrospect the results of nearly a century of microscopical study of the gland-cell, and more particularly the results of the last fifty years, it is not difficult to see that the cytology of glandular secretion has been almost invariably approached from the wrong starting-point. Instead of beginning with a secretory droplet about to be expelled from the cell, and tracing it back step by step to the material of its origin, we have all too frequently started from some morphological expression of presumed cellular activity and achieved the production of secretory droplets by a single leap—usually speculative. Doubtless this method of approach was largely the result of necessity, since the study of the secretory droplets themselves always ended in frustration exactly at the critical point of their first appearance, due to the inadequacy of technical methods of demonstration.

Now, however, that the various elements of the story have been painfully accumulated, there seems to emerge at last a consistent explanation of the cytological phenomena. Secretion is in essence a phenomenon of 'granule' or droplet formation. Starting with a single such secretory droplet about to be expelled from the cell, we find it possible to trace its origin step by step to a minute vacuole, which has thus from the beginning served as a segregation center for a specific secretion-material. The primordial vacuole is found to arise in that zone of the cell characterized by the presence of the Golgi apparatus, and the evidence indicates, if it does not demonstrate, that the primordial vacuole arises through the activity of the Golgi substance and undergoes a part at least of its development in contact with, or embedded in, the Golgi apparatus. Concerning the place and mode of synthesis of the secretory substances peculiar to a specific kind of secretory-droplet, we have as yet no very tangible understanding. Apparently the Golgi apparatus plays some immediate rôle in the process of accumulation and final synthesis of the secretion-product, but the concomitant changes in other cellular structures suggest that all parts of the cell contribute in some way. This very probably means that the chondriosomes (and ergastoplasm, if any) are concerned in some indirect manner which is not registered in their morphological history; and further, that the nucleus cooperates in some way with the cytoplasmic area, as registered by its various changes in position, shape, chromaticity, etc. Concerning the exact nature of this nuclear contribution, however, nothing definite can be stated, except that the evidence distinctly indicates that nucleolar extrusions or the other direct nuclear emissions so commonly described in the literature, do not usually play any direct part in the production of a secretory droplet. It may even be doubted whether their occurrence has anything to do with the essential processes of secretory synthesis.

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STUDIES ON THE PHYSIOLOGY OF A GENE

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THE GENES AS AGENTS OF CONTROL IN DEVELOPMENT

IN THE organism the genes play a dual rôle. As essential components of sperm and egg they constitute the known elements of heredity. But they also serve in some measure to control the course of events during development. Genetics treats of them only in the first capacity. In studies on inheritance there is little need, as a general rule, for noting the effects of a gene on the individual except for some single distinctive change. It is only necessary to have a definite external sign indicating the presence of the particular factor in question. Further than this genetics, strictly speaking, is not concerned with the physiological activities of the units with which it deals.

The problems of development have been approached along independent lines. The embryologist has undertaken an analysis of the orderly sequence of events by which the egg becomes a more or less highly differentiated organism from a point of view and by methods which are peculiar to his own field. Current hypotheses offered to account for the phenomena observed have been constructed without reference to the gene. It would appear, however, that there is an increasing measure of interest in the view that no theory of development is of requisite breadth which does not take into consideration the directive influence of the gene complex.

Concerning the nature of gene action, however, our ignorance is almost complete. Knowledge of the genes as hereditary units has passed far beyond an understanding of these entities in their equally important relation to the developmental process.

The student of heredity has long seen in the sharply discontinuous effects of many alternative genetic factors a possible line of attack upon developmental problems. The races he deals with may be looked upon as physiological systems differing in one or more discrete germinal units. He has seen again and again that certain clear-cut changes in the phenotype follow upon the substitution of one allelomorph for another. Might it not be possible, he asks, to trace out the chain of physiological processes linking the superficial effect to the hereditary factor? Such analysis, if successful, should add greatly to an understanding of the character of developmental processes.

In the literature of heredity there is abundant evidence to show that the genes are capable of very precise regulation of developmental phenomena. Factors are known affecting all stages in the ontogenetic cycle and it is a well recognized fact that their action may be large or small. Quite aside from the profound insight it has afforded into hereditary phenomena is it not, in fact, one of the triumphs of modern biology to have uncovered in the gene complex an orderly, albeit complex mechanism within the cell which guides and controls the manifold processes of the living substance?

In view of the paucity of definite evidence, one can form at present no more than a hazy picture of the real significance of the gene theory for phenomena other than those it was directly invoked to explain. Imagination, therefore, should not be given too free a rein. But to the writer, and I am sure there are other geneticists who hold a similar view, the resolution into its constituent units of one of the two main variables with which the developmental physiologist deals, namely, heredity, can not but mark a very important step forward in opening up new paths by which the problems in this field may be attacked.

In a thoughtful article F. R. Lillie (1927) has recently discussed the mutual relations of genetics and the physiology of development. There is much of interest in the paper that must be passed over here, but I should like to advert briefly to one point of particular importance concerning the possibility of effecting a liaison between these two divisions of biological science. To quote from Lillie's paper, "The progress of genetics and of physiology of development can only result in a sharper definition of the two fields, and any expectation of their reunion (in a Weismannian sense) is in my opinion doomed to disappointment. *Those who desire to make genetics the basis of physiology of development will have to explain how an unchanging complex can direct the course of an ordered developmental stream.*" (Italics mine.) Lillie grants that genes are concerned in the origin of all characters in the organism but regards the widely accepted genetic doctrine that each cell contains the entire complex of genes as a stumbling block to an explanation of differentiation by the action of genetic factors. This, it must be admitted, is a fundamental difficulty. If it cannot be resolved there seems little hope of explaining development on the basis of the genes as primary agents of control and studies of the type to be discussed later in this paper would be futile.

One should not attempt in the present state of our knowledge to formulate a general theory of development based upon gene action which would bridge the gap. There is as yet no adequate basis of fact for such a venture. But it is certainly pertinent to inquire if there is anything illogical or inconsistent in the view that the genes, though the same in every cell, can yet serve as the primary source of control of the highly complex series of changes which these cells undergo in development. I can not find that there is.

It might reasonably be supposed that the genes call forth a consecutive series of reactions, each reaction providing the necessary physiological basis for the succeeding one. Each gene becomes functional when its appropriate substratum emerges in response to the activity of genes already in play. The phenotypic effects show that there is wide diversity in the properties of the individual hereditary elements and it is a logical inference that each gene requires certain specific intra-organic environmental conditions in order to function. If this be granted it follows that the genes will come into action in orderly sequence. While the genes are the same in every cell they will function in an ever-changing way as they alter the circumstances under which they operate. According to this hypothesis each gene comes into play only upon the completion of certain earlier events primarily controlled by other genes. Each factor may not be physiologically active at all stages. Some genes may be narrowly restricted in their operations; others may function over a wide range of ontogenetic conditions. At one stage in development a particular gene may act in one way and at another stage in a different manner because the milieu has been changed in the interval.

The criticism may be advanced that this view, if sound, merely shifts the problem one stage farther back. But, in a sense, this is all that any scientific explanation can do. We know little concerning the principles governing the unity and integrity of the gene complex in a given species or the specific physiological inter-relationships between the component elements. No answer can be given to the question why certain aggregates of genes form functional sets which come to expression as organisms and others fail to appear as units in the living world. In view of the mathematical possibilities which the genes offer, and granting natural selection, is it not in fact a little surprising that organisms are no more variable than they are? It seems likely that there are laws involved here of first importance for an understanding of developmental processes. Of these we can only express our ignorance and wait for what future investigations may bring forth.

The suggestion that the genes, though remaining the same in every cell, may nevertheless govern differentiation by series of chain reactions, each reaction changing the substratum upon which the gene complex impinges, which, in turn, opens the way for further physiological events, will strike the chemist and the physiologist with a familiar ring. Workers in each of these sciences might furnish numerous examples of systems of this sort in which the essential steps have been determined. It is recognized, of course, that the most complex system with which the physiologist deals is infinitely simpler than the totality of changes involved in development. In the latter we have not only the primary effects of an undetermined number of genes to account for but also a host of side reactions between elements of higher and higher order emerging during the ontogenetic process.

MODE OF ATTACK

Elsewhere the view was expressed (Brink, 1927) that the genes whose primary physiological action should prove most accessible to analysis are those which come into play under conditions in which they do not impinge upon a large number of processes and thus obscure their main properties by secondary effects. Genes conditioning specific reactions late in development should provide, in general, the most suitable material since these encounter the fewest physiological cross-currents. The earlier in ontogeny that a primary differential reaction occurs the greater the likelihood, other things being equal, that some subsequent change will conceal it. Genes directly affecting the character of some end-product in the organism should be particularly suitable for study. Factors controlling the production of certain pigments and especially reserve food materials in plants fall in this category.

THE WAXY GENE IN MAIZE

It was upon the basis of these considerations that the writer in 1925 began a study of the physiological action of the waxy gene in maize (*Zea mays*). Through the changes it occasions in the pollen reserves the waxy gene alters the rate of development of the male gametophyte. This circumstance affords a rather unusual opportunity for observing the phenotypic effects of the factor. The forepart of the present paper is devoted to a consideration of the results on this phase of the study. In an effort to penetrate further into the physiology of the gene, certain biochemical investigations on the nature of the reserves formed under the action of the waxy factor and the enzyme accompanying them were undertaken. This more difficult aspect of the problem is dealt with in the latter part of the article. The results of the two lines of investigation supplement each other in pointing to the way in which the waxy gene probably functions during development.

The waxy character was first noted by Collins (1909) in some corn received from China. Collins observed that the endosperm of this race differed in texture from that of other varieties of maize. In the mature condition it possesses some of the physical properties of a hard wax and was consequently termed "waxy." In inheritance the waxy character behaves as a simple recessive to the non-waxy condition. Weatherwax (1922) discovered that the endosperm reserves of waxy seeds form a reddish-brown compound when treated with dilute iodine, a characteristic which serves to distinguish this race from all other known forms of maize.

Demerec (1924), Brink and MacGillivray (1924) and Longley (1924) found that the waxy gene affects the character of the pollen also. Whereas the starch granules in the pollen of ordinary races of maize give the typical blue reaction with iodine, the corresponding bodies in pollen from waxy plants assume a reddish-brown color when similarly treated. A parallel difference in the carbohydrate reserves in the embryo sacs was later established (Brink, 1925). In the embryo, leaves, stem, floral organs and other parts of waxy plants the starch grains are identical with those in normal plants in giving a blue color with the iodine reagent. Waxy plants are indistinguishable in appearance from the non-waxy type in the field. The gene, therefore, does not occasion any changes of a general nature in development. Its activity appears to be confined entirely to starch metabolism and is further restricted in that only the reserve starch in pollen, embryo sac and endosperm is affected. The so-called starch of translocation formed in the vegetative parts is the same in waxy and non-waxy plants, at least so far as the iodine test reveals. From the standpoint of accessibility to physiological analysis the localized action of the waxy gene is an important consideration.

Observations on the effect of the waxy gene in the male gametophyte have revealed the significant fact that hybrids between waxy and non-waxy plants produce two kinds of pollen in equal numbers. The one class, staining blue with iodine, corresponds to that formed by the non-waxy parent; the other group, giving a reddish-brown color, is identical with the pollen of waxy plants. In the flowering plants the reduction divisions occur at sporogenesis. It is a logical inference that in the case of these heterozygous waxy plants the one class of pollen grains has received the non-waxy gene and the other equally frequent group, the waxy factor, and that these allelomorphs exert a direct effect in the gametophyte generation.

The gametophyte in the higher plants is a vastly simpler structure than the highly differentiated sporophyte. Manifestation of the action of the waxy factor in the pollen makes possible a study of the physiological properties of this gene without reference to the complications which surround its action in the much specialized diploid plant. And the fact that the gene produces its characteristic effect in the pollen but two cell generations removed from the reduction divisions indicates that its action may be of a direct sort. That is, the chain of events between end result and the gene may be, comparatively speaking, short and direct.

Effect of the waxy gene on pollen-tube growth

Extensive studies on the inheritance of the waxy character by Collins and Kempton (1911) and byKempton (1919) show that, on the average, a deficiency of waxy seeds larger than can reasonably be ascribed to chance occurs when heterozygous waxy plants are self-pollinated. On the Mendelian basis 25 per cent of the seeds are expected to be waxy; only about 24 per cent are obtained. This result has been confirmed by a number of investigators. When heterozygous waxy plants are used as staminate parents in combination with the recessive waxy type (*wx wx* ♀ × *Wx wx* ♂) significantly fewer than 50 per cent of the seeds formed are waxy. In the reciprocal cross (*Wx wx* ♀ × *wx wx* ♂) the distribution is in close agreement with Mendelian expectation.

Kempton (1919) suggests that the deficiency of waxy seeds in the above types of matings "could be brought about by a higher death rate for the gametes with the waxy character, or a less vigorous growth of the pollen tubes of such gametes, or a failure of the plants to form the gametes in equal numbers." It has been shown by Brink and MacGillivray (1924) and by Brink (1927) that heterozygous plants produce equal numbers of the two classes of pollen grains within the limits of random sampling, so that the aberrant ratios can not be accounted for on this basis. When it was discovered that *Wx wx* plants produce two equally frequent classes of pollen, the one kind staining bluish with iodine, like that of the non-waxy parent, and the other, reddish-brown as in the waxy variety, Brink and MacGillivray (1924) suggested that the deviation from expectation on Mendelian grounds was probably caused by a differential rate of development of the two classes of male gametophytes. The difference in the character of the reserve materials in the pollen might well provide the chemical basis for such a phenomenon. Thus far attempts actually to follow the progress of pollen tubes in the style of maize have not been successful so that direct proof of this hypothesis is lacking.

If there were a *constant* difference in the rate of growth of waxy and non-waxy pollen tubes in the style we should expect to find a smaller proportion of waxy seeds in the lower half of the ear than in the upper. The farther the pollen tubes travel the greater should be the tendency for the two classes to become separated. Counts on numerous ears show that in general, however, the percentages of waxy seeds on the two halves of the ear are not significantly different. This holds even when the deficiency of waxy seeds is relatively large, as in *Wx wx* plants homozygous for the sugary gene, to be discussed below.

Brink and Burnham (1927), in offering an alternative explanation, point out that two stages in the development of the pollen tube may be recognized. During the first of these the needs of the growing tube are met by the food reserves contributed by the pollen grain, while subsequent elongation is dependent upon supplies from the style. Direct observations on pollen tubes of a number of other species growing on artificial media indicate that the first period is a relatively short one, the pollen reserves being quickly consumed even in the presence of an abundance of nutrients in the culture solution. It is suggested that the waxy gene exerts a differential effect during the first stage of pollen tube growth only, that is, while the gametophyte is dependent upon its own reserves. During subsequent growth it is assumed that the waxy and non-waxy pollen tubes develop at the same rate.

Support for this view is seen in the fact that the food materials in pollen and style are different. The pollen contains considerable amounts of starch and also fats; the style on the other hand is starch-free, the principal reserves being sugars. Now it has been shown that the waxy gene affects the power of the plant to synthesize starch and it may be inferred that the factor also modifies the reverse process, namely, starch hydrolysis. On this hypothesis there is a chemical basis for differential development of the waxy and non-waxy gametophytes in the early stages of pollen tube growth only.

In the attempts which have been made to explain the deficiency of waxy seeds following combinations in which *Wx wx* plants are used as pollen parents the fact that the ratios on ears from different plants frequently show rather wide fluctuations from the mean value of the population has received particular attention. Kempton (1919) first showed, and his results were confirmed by Brink (1925), that the distributions on ears from matings of this kind do not always form a homogeneous group. The variability in proportion of waxy seeds on individual plants is frequently too high to result from the operation of chance alone. The writer has extensive unpublished data on this situation, which, however, do not point to any satisfactory explanation of the problem. It is reasonably clear that environmental conditions as well as genes other than the waxy-non-waxy pair affect the waxy ratio. No one, however, has yet succeeded in identifying the individual factors at work in either of these complexes. Kempton's (1927) conclusion that storing the pollen from *Wx wx* plants greatly increases the proportion of functioning waxy gametes is not supported by the unpublished results of a recent experiment made by Miss Thelma McWilliams and the writer. In fact our tests showed the opposite effect, namely, that aging the pollen tends to further lower the proportion of effective waxy pollen grains.

In certain of the results obtained by Kempton (1919), Mangelsdorf and Jones (1926) see evidence for the occurrence of an accessory factor linked with the waxy gene which differentially affects the rate of growth of waxy and non-waxy pollen tubes. Indeed these workers assume that the waxy gene itself has a neutral influence and that the disturbances in the waxy ratio are wholly due to an accessory factor. If this explanation is sound the basis upon which the investigations discussed in this paper rest, namely, that there is a causal relationship between the nature of the carbohydrate reserves in waxy pollen and the deficiency in the waxy ratio, is quite false.

One looks in vain, however, for any definite support of their hypothesis in the data Mangelsdorf and Jones use. Kempton's F_2 progenies from selfed *Wx wx* plants gave an average of 23.7 per cent waxy seeds and the F_3 progenies, an average of 24.6 per cent waxy seeds. According to Mangelsdorf and Jones, "The difference between these two generations is 4.3 times the probable error and would be expected as the result of chance only once in about 267 trials." Such a difference, they continue, cannot be explained by the action of the waxy gene itself, but is exactly what would be expected if an accessory factor linked with the waxy gene is involved. Are the authors justified in their conclusion, however, that the difference in percentage of waxy seeds in the two generations is actually a significant one? It would appear from the result arrived at that the difference has been evaluated in terms of a probable error based upon the familiar Mendelian formula for three to one ratios. But Kempton (1919) himself has shown that the percentage of waxy seeds on the individual ears comprising the two respective populations upon which the net values of 23.7 per cent and 24.6 per cent are based, do not form homogeneous groups. In other words, the values vary around more than one mean. Now the probable error formula mentioned above, which Mangelsdorf and Jones have apparently used, is legitimately applied to massed data only when the conditions determining the appearance of the two classes of segregates are essentially the same in each of the subgroups comprising the population. This requirement is not fulfilled by the material under consideration, as Kempton (1919) has clearly demonstrated. Mangelsdorf and Jones, in ignoring this circumstance, have been misled into attaching a significance to the difference between the F_2 and the F_3 which is not justified by the facts; the probable errors they have used are too low. Moreover, the direct comparison of F_2 and F_3 data obtained from plants grown in two successive years is a doubtful procedure in view of the likelihood that environment conditions affect the waxy ratio to some extent.

Mangelsdorf's (1929) recent use of the same method in evaluating a net difference in the proportion of sugary and non-sugary seeds on ears with long styles and short styles is open to the same criticism. The case is somewhat similar to the waxy one in that the stock appears to involve a gene affecting pollen tube growth. The number of ears which Mangelsdorf obtained is relatively limited. The large variation in the percentage of sugary seeds on the individual ears indicates that Mangelsdorf's conclusion regarding the significance of the difference between the average values for the long-styled and short-styled series may rest upon less secure ground than he assumes.

Mangelsdorf and Jones (1926) find further evidence for their view that the deficiency of waxy seeds is due to an accessory factor linked with the waxy gene in some results which Kempton (1919) has presented on the relative percentages of waxy seeds given by a series of plants on being selfed and intercrossed. It is noted that heterozygous individuals which give less than 25 per cent waxy seeds on selfing tend to show a similar minus deviation when used as pollen parents in intercrosses. Likewise, plants which give a normal ratio on being self-pollinated tend to give a like result when crossed on sib plants. Using a limit set by a minus deviation equal to twice the probable error, Mangelsdorf and Jones place the plants tested in this way in two groups, low and normal, comprising respectively, 10 and 14 individuals. They assume that this distribution arises as a consequence of heterozygosity in one of the parents of Kempton's hybrids for an accessory factor affecting the chances of waxy and non-waxy gametes in accomplishing fertilization. This appears to be an exceedingly slender thread upon which to hang such an hypothesis. If it be admitted that the correlation in the waxy ratios of selfs and intercrosses is entirely due to the inherent character of the pollen parents—and this is open to some question—it does not follow that the results are attributable to the action of an accessory factor linked with the waxy gene. Other explanations not involving linkage as plausible as the one Jones and Mangelsdorf suggest might be set forth. It has been found by Brink and Burnham (1927), for example, that heterozygous waxy plants homozygous for the sugary gene (*su su Wx wx*) give markedly lower waxy ratios when used as pollen parents than do sibs carrying the non-sugary factor (*Su Su Wx wx* or *Su su Wx wx*). When pollen from the double heterozygote, *Su su Wx wx*, is applied to the double recessive the ratio of waxy seeds in the sugary class is no lower than that in the non-sugary class. In fact the same proportions of waxy seeds are obtained in both classes as in *wx wx* ♀ × *Wx wx* ♂ combinations not involving the sugary gene. This shows that the sugary gene affects the waxy ratio indirectly through some action on the parent sporophyte. Gametes of the types *su Wx* and *su wx* behave differently according to whether the diploid plant from which they are descended is homozygous sugary or carries one dose of the non-sugary gene. This case has been thoroughly studied and shows very clearly that genetic factors may very significantly modify the waxy ratio without acting as differentials in the gametophyte generation. It is quite possible that a part of the variation investigators have found in populations of ears segregating for the waxy character is due to genes acting in the same way as sugary.

The results obtained in the above mentioned studies on the effect of the sugary gene afford additional evidence for the conclusion that it is the waxy factor itself and not a gene linked with it which is primarily responsible for modification of the Mendelian distribution. As has been pointed out elsewhere (Brink, 1927) the deviation in the waxy ratio on single ears in sugary stocks is usually large, obviating much of the difficulty in classifying individuals with respect to departures from the normal value. If the sugary gene were interacting with a gene linked with waxy rather than with the latter factor itself we should expect the waxy ratios in sugary lines to be grouped around three modes, a high, a low and a normal. Tests with 128 different *su su Wx wx* plants in three distinct stocks showed, however, that the waxy ratio was low in 125 cases and not significantly different from normal in the remaining three. When, therefore, the aberrant results obtained in waxy lines are "exaggerated" by introducing the sugary gene in homozygous condition still clearer evidence is obtained that the deficiency of waxy seeds regularly follows the waxy gene.

A condition similar to or identical with, that characteristic of waxy maize has also been described in a few other members of the grass family. Gris (1860) found it in *Oryza sativa* var. *glutinosa*, and Meyer (1886) reports it in *Panicum miliaceum* var. *canditum glutinosum* and *Sorghum vulgare glutinosum*. Longley (1924) notes that it also occurs in *Coix lachryma-jobi*. Parnell (1921) selfed nine F_1 plants following a cross between glutinous and a non-glutinous variety of rice, obtaining 6879 seeds, of which 1587 were of the glutinous type. On the monohybrid basis 1720 individuals of the glutinous sort would be expected, or 133 more than were obtained. Brink and MacGillivray (1924), in calling attention to the statistical significance of this deficiency, suggested that there is a selective action of some sort which discriminates against fertilization by male gametes carrying the glutinous factor. Chao (1928) has made a careful analysis of this case and has shown that, in general, heterozygous glutinous plants produce fewer seeds of the recessive type than are expected on the Mendelian basis. The probable explanation of the deficiency, according to Chao, lies in a lower rate of growth of the pollen tubes carrying the glutinous factor and is to be attributed to some property inherent in the glutinous gene itself. It is a significant fact that the glutinous character in rice, showing changes in the carbohydrate reserves of endosperm and pollen apparently identical with those in waxy maize, should also involve differential development of the male gametophyte. The parallel behavior of waxy maize and glutinous rice heterozygotes in producing a deficiency of recessives strengthens the view that the genes which are the cause of the change in the nature of the reserves are also directly responsible for modification of the ratio.

In any consideration of the possibility that the irregularities in the waxy ratio may be primarily due to a gene other than waxy the clearly established fact that the latter factor occasions a pronounced differential effect in the male gametophyte which may be demonstrated in the pollen grain by the iodine test should be given due weight. Since the action of the factor is on the food reserves which are directly consumed in the formation of the pollen tube, just the sort of situation is provided which one would expect to lead to a difference in rate of development of waxy and non-waxy gametophytes. This circumstance alone puts the burden of proof squarely upon those who, like Mangelsdorf and Jones, hold a different view.

Summary of the phenotypic effects of the waxy gene

1. The waxy gene is definitely localized in its activity, so far as it has been possible to discern, to the endosperm, the pollen and the embryo sac. It does not occasion any change in the size or form of the plant.

2. In the endosperm, pollen and embryo sac of waxy plants, the carbohydrate laid down differs from that in the same parts of common maize in staining reddish-brown with iodine rather than blue.

3. The starch grains in the other parts of waxy plants such as the embryo, stem and leaves give the typical blue reaction with iodine. So far as can be detected, therefore, the effect of the waxy gene is restricted to the reserve starch only.

4. Heterozygous waxy plants produce two classes of pollen in equal numbers. The starch grains in the one group stain reddish-brown with iodine like those of the waxy race, while the starch grains in the other class give the blue reaction of ordinary starch. This clear-cut effect of the waxy gene in the pollen immediately following the reduction divisions suggests that the gene controls some step in the synthesis of the reserve corbohydrate in a direct and precise way.

5. When plants heterozygous for the waxy gene are self-pollinated or used as staminate parents in crosses with the recessive type a slightly smaller proportion of waxy seeds is formed than is called for on the Mendelian basis. The deficiency is attributed to a lower rate of growth of waxy pollen tubes during the early stages of development when they are dependent upon the reserves stored in the pollen grain.

BIOCHEMICAL STUDIES

The non-waxy and waxy allelomorphs may be looked upon as conditioning a reaction or series of reactions leading, in the one case, to the production of common starch and, in the other, to a carbohydrate of a somewhat different nature, as the iodine test shows. These substances are the final terms in the chain of physiological processes upon which the genes impinge. They are likewise end-products in the general economy of the plant, for they mark the last step in the preparation of pollen and seed for the initiation of new cycles of development. Stored in insoluble form, they remain definitely out of play until conditions favorable for germination of pollen and seed are met. They are then brought back into the current of metabolic activity by a reversal of the reactions involved in their synthesis. The processes in which this pair of genes is concerned, therefore, are arrested by natural means immediately following the stage at which the factors manifest their differential action. This circumstance is of obvious importance from the standpoint of accessibility to physiological analysis. One is enabled thereby to approach directly the particular change for which the waxy gene is responsible.

In analysing the physiological properties of the waxy gene we have sought first to determine the way in which the peculiar carbohydrate formed in waxy plants differs from common starch. And, secondly, an attempt has been made to find the mechanism responsible for this change.

Preparation of the waxy endosperm reserve carbohydrate in pure form

By adapting the essential steps in the commercial manufacture of maize starch to laboratory conditions, Brink and Abegg (1927) have obtained the reserve carbohydrate occurring in the endosperm of waxy seeds in relatively pure form. The operation is somewhat tedious, but a very effective separation of the extraneous materials can be made and the refined carbohydrate obtained in quantity. The nitrogen content of the purified product was 0.013 per cent on the dry basis. Starch prepared from common maize by the same procedure contained 0.035 per cent nitrogen. These values compare very favorably with the proportion of nitrogen in commercial samples of maize starch.

Form of the granules in waxy pollen and endosperm

The endosperm reserves in the waxy variety are organized in granular form, as in common maize. In both types the particles are of similar size and are disc-shaped with a centric hilum. The waxy granules are slightly more angular in outline than those of the other type. In common maize the starch grains in the pollen are much smaller than those in the endosperm, seldom measuring more than $4\mu \times 1.5\mu$ through their main axes. They are regularly ovoid in shape. In waxy pollen, on the other hand, the granules are frequently dumb-bell shaped but show considerable variation. When examined under polarized light the granules from the endosperm of non-waxy and waxy maize show no clear differences. In both types the figure is usually centric and the lines are commonly at right angles to each other. The bands are possibly more clearly defined in the case of the waxy material.

The two classes of granules react very differently when treated with strong alkali or concentrated chloral hydrate. The form of the waxy sort is much more quickly distorted. The swelling properties in water differ also, but little attention has been given in these studies to the colloidal characteristics of the two carbohydrates.

Color reaction with iodine

Starch from the endosperm of ordinary maize, in common with that from most other sources, forms an intense blue color when treated with the common iodine reagent (1.0 per cent KI, 0.3 per cent I, in aqueous solution). The corresponding substance from the endosperm of waxy seeds when similarly treated gives a compound which is reddish-brown by reflected light. Pastes containing 0.1 per cent of the two reserve materials likewise react very differently to the iodine test. If 5 drops of the iodine solution are added to 10 cc. samples, ordinary starch paste gives a color by transmitted light described by Ridgway (1912) as Helvetia Blue, whereas the waxy material gives Rood's Violet. The difference is not obliterated by varying the proportions of the reacting substances over a wide range. Similar preparations using the granular reserves of the pollen give the same respective color reactions, namely, Helvetia Blue and Rood's Violet. In its reaction to iodine the waxy reserve substance is quite similar to glycogen.

The color reactions between starch and iodine have been studied from the colloidal standpoint by Harrison (1911). He found that any agency such as alcohol, potassium iodide or heat which tends to increase the degree of dispersion of the iodine particles shifts the color in the direction of blue to red. On this view the ultimate particles of which the waxy reserve is composed would appear to be smaller than those of common starch, thus presenting a greater surface upon which the iodine is distributed. The smaller size in the case of the waxy substance might be the result of a lower degree of "association" of some element common to both the waxy and non-waxy carbohydrates. The term "association" as used in this connection refers to a union between molecules dependent upon some force other than chemical valency.

Proximate analysis of waxy and non-waxy seeds

On the basis of its color reaction with iodine, Weatherwax (1922) concluded that the reserve material in the endosperm of waxy maize is erythrodextrin. This term was first used, it appears, by Brücke (1872), who applied it to the product obtained on roasting starch. Lintner and Düll (1893) contended that roasted starch contained a mixture of dextrins and, by repeated fractional precipitation with alcohol, claim to have prepared a pure erythrodextrin. The substance gave a reddish-brown reaction with iodine, as its name suggests, and, like Brücke's preparation, was readily soluble in water. The reserve carbohydrate in the endosperm of waxy maize gives the reddish-brown color reaction by reflected light but Brink and Abegg (1926) show that it is not soluble in water or in 10 per cent alcohol. The waxy reserve, therefore, does not conform to either of the substances previously described as erythrodextrin.

TABLE 1

Percentage amounts of starch, dextrin and sugar in waxy and non-waxy maize seed based on dry weight

	STARCH		TOTAL SUGARS
Non-waxy............	57.85	0.90	.42
Waxy................	59.93	1.87	.70

TABLE 2

Percentage amounts of starch, dextrin and sugar in waxy and non-waxy maize pollen based on dry weight

			TOTAL SUGARS
Non-waxy.	16.28	2.25	10.27
Waxy.....	14.96	2.24	11.57

Meyer (1886), in describing a similar substance found in the endosperm of *Panicum miliaceum* var. *canditum glutinosum* and *Sorghum vulgare glutinosum*, terms it "red-staining starch." Our own investigations on the reserve material in waxy seeds show that the substance is essentially starch-like in nature and we have applied to it the convenient term, waxy starch.

The results of proximate chemical analyses of waxy and non-waxy seeds are clearly not consistent with the view that the principal reserve material in the waxy endosperm is a dextrin (Brink and Abegg, 1926). In Table 1 the relative amount of starch, dextrin and total sugars in the seed of waxy and non-waxy maize as determined by the standard method is shown.

The separation of the dextrin fraction from the starch is based upon the solubility of the former in 10 per cent alcohol after removal by appropriate means of the fatty substances and the sugars. It may be seen that the principal carbohydrate of the waxy seed, far from falling in the dextrin group, appears in the starch class. In fact the content of starch in the waxy seed is somewhat higher than that in the non-waxy material. The absolute quantities of dextrin in both kinds of seed are small, amounting to less than two per cent of the dry substance.

Analyses of the pollen from waxy and non-waxy plants reveal a similar situation, as shown in Table 2. The pollen contains a higher proportion of sugars and only about one-quarter the amount of starch found in the endosperm. The important point is, however, that in the two types, waxy and non-waxy, starch and dextrin are present in about the same proportion and that the former is the chief carbohydrate reserve in both.

Composition of the starch grain

Since Nägeli's (1858) pioneer work it has been recognized that the starch grain is not composed of a single homogeneous substance. Meyer (1895) described two constituents which he termed α-amylose and β-amylose, respectively. The former is mainly responsible for the viscosity of starch pastes and is comparatively resistant to diastatic hydrolysis. On the other hand, β-amylose gives a limpid solution in hot water, stains intensely blue with iodine and is quickly converted to maltose by diastase.

Numerous means have been tried to separate the two components. Sherman and Baker (1916) found that when one per cent raw starch was gelatinized in water at 85°C. and centrifuged at the rate of 2400 r.p.m. for 30 minutes in the presence of 0.001 M NaCl it is separated into a lighter, clearer and more limpid layer containing the more soluble constituent, β-amylose, and a heavier, more viscous layer containing the less soluble component, α-amylose.

Common maize starch when treated in this way (Brink and Abegg, 1926) separates into two distinct layers, as Sherman and Baker found in their experiments. The upper layer is comparatively clear and contains only about 8 per cent of the starch present, and the lower is thick and viscous. Waxy starch gives a very different result. It also separates rather distinctly into two portions but the relative volumes occupied by the two layers in the tube and the amounts of starch they contain are quite unlike those in the former case. The upper layer in the centrifuged tube of waxy starch paste is less deep than the corresponding portion of the non-waxy tube but contains about 60 per cent of the total dry matter. The lower layer is much less viscous than the α-amylose fraction of non-waxy starch.

When tested with iodine, both constituents of the waxy starch paste give the color described by Ridgway (1912) as Rood's Violet, whereas the preparations from the non-waxy starch stain the familiar blue. It is clear, therefore, that the difference between the waxy and non-waxy starches is not to be accounted for on the assumption that they are composed of the same two substances but in different proportions.

A biochemical method (Ling and Nanji, 1923) designed to measure the relative proportions of α- and β-amylose in starch has given different results with this material than the procedure of Sherman and Baker. According to Ling and Nanji, the weakly acting amylase of the resting barley grain, extracted with water and precipitated with alcohol, converts the β-amylose to maltose while the α-amylose portion is scarcely attacked. Duplicate tests on common maize starch, using the precipitated barley diastase method, gave 48 per cent and 47 per cent respectively of the starch hydrolyzed to sugar. A sample of waxy starch paste showed 49 per cent of the starch converted (Brink, 1928). The barley diastase method, therefore, reveals little difference in the content of β-amylose in common and waxy starch. According to this test there appear to be approximately equal amounts of α-amylose and β-amylose in both.

Evidently the centrifugation method of Sherman and Baker and the barley diastase method of Ling and Nanji measure different things. The biochemical test indicates no important difference in the relative amounts of α- and β-amylose; but the substances may occur in quite dissimilar physical conditions in the two starches, accounting for the different results on centrifugation. About 60 per cent of the waxy starch remains in the upper layer of the tube and the lower layer occupies a volume nearly four times that of the corresponding fraction in the non-waxy sample. This indicates that the particles in both fractions of the waxy starch paste are smaller than those in the corresponding portions of the other lot.

Hemicellulose in waxy and non-waxy starch

Schryver and Thomas (1923) have identified a third substance in starch, which they have shown to be a hemicellulose. When a starch paste is treated at 50°C. with malt amylase there appears, in 10 to 30 hours, depending upon the enzyme concentration, a flocculent precipitate. This is the hemicellulose. It gives a blue coloration with iodine but resists digestion on prolonged treatment with amylase. It is not known whether hemicellulose is an integral part of the starch grain or is present as an impurity.

In the present studies it was not possible to make a quantitative estimation of the hemicellulose content of the waxy and non-waxy starches on account of the rather small supply of laboratory-prepared material available. It was evident, however, from the relatively clear appearance of the conversion liquids in a series of tests on rate of hydrolysis of waxy starch with malt amylase that this substance contained practically no hemicellulose. In common maize starch, on the other hand, significant amounts of it are present. Schryver and Thomas (1923) report 3.6 per cent.

The presence of hemicellulose in common maize starch makes it impossible to measure the rate of conversion of the latter substance to maltose under the action of a hydrolytic agent by noting the time required for the solution to lose the power of giving a color reaction with iodine. Owing to the hemicellulose present color is shown by the conversion liquid long after the starch has been digested. In our first experiments (Brink and Abegg, 1926) on the comparative rate of hydrolysis of waxy and non-waxy starch by HCl and by salivary amylase the work of Schryver and Thomas on hemicellulose was overlooked and we were led to erroneous conclusions through the use of a method which is now recognized as inadequate. We found that non-waxy starch paste on treatment with these two hydrolytic agents retained the power to give color with iodine significantly longer than did waxy starch paste and inferred from this result that the latter substance was more easily digested. It appears, however, that the difference may have been due wholly to the fact that the common maize starch contains a considerable amount of the resistant, blue-staining hemicellulose, whereas the waxy starch is almost free from it.

The sugar formed on treating waxy and common maize starches with amylase

While a number of investigators dissent from the conclusion, the view is widely held that, under the action of amylase, starch is split quantitatively into a single sugar, maltose. Pringsheim (1923) does not consider that satisfactory proof of the formation of but one sugar has been furnished, and Armstrong (1924) believes that the starch molecule contains glucose as well as maltose residues. Ling and Nanji (1923) are more specific. They claim to have shown that, on hydrolysis with malt amylase, β-amylose (amylose) forms maltose, and α-amylose (amylopectin) produces two sugars, maltose and isomaltose. The weight of evidence, nevertheless, seems to be in favor of the conclusion expressed by Maquenne and Roux (1905) that starch is composed entirely of maltose residues.

In determining whether the reserve starches of waxy and non-waxy maize differ with respect to the sugar formed on diastatic hydrolysis the conversions were carried out in two stages. The starch paste was first treated with alcohol-precipitated barley amylase which hydrolyses the β-amylose and leaves the α-amylose practically unchanged. The latter substance was then separated from the other products of the initial conversion and hydrolysed with a very active preparation of malt amylase. The sugars obtained were identified by their reducing power, specific rotation and the osazone test. The detailed procedure is given in a recent paper (Brink, 1928).

β-amylose fractions of the common and waxy starches

After treatment of the starch paste with barley diastase for 24 hours at 50°C. the conversion is stopped by boiling. The liquid is evaporated to a small volume and poured into alcohol, giving a final concentration of 60 per cent. The α-amylose is precipitated and filtered off. The filtrate, containing the conversion products of the β-amylose, is further purified by treatment with 90 per cent alcohol. The concentration or total solids in solution is obtained by the specific gravity method. The reducing power may then be measured iodimetrically and the specific rotatory power determined. In the case of the β-amylose fraction of the common maize starch the constants were as follows: R(reducing power) = 93 and $[\alpha]_D$ (specific rotation) = +144.6°. The corresponding values for maltose are R = 100 and $[\alpha]_D$ = +138°. It seems probable from these results that some material of a dextrinous nature was still present in the solution after the treatment with 90 per cent alcohol. Dextrins would tend to lower the reducing power and increase the specific rotation. On preparing the osazone a clear test for maltose was obtained. A trace of glucosazone was also found but no crystals of the *iso*malt osazone type described by Ling and Nanji (1923) were present. On the basis of these results it is concluded that the sugar formed from the β-amylose portion of non-waxy maize starch is maltose, accompanied by a very small amount of glucose.

The sugars formed on treating waxy starch paste with barley amylase were examined in the same way. The filtrate obtained after precipitating the α-amylose was milky in appearance and proved difficult to clear. It gave a violet reaction with iodine, showing that some unconverted dextrins were still present in a very fine state of division. The constants determined on the solution were as follows: R = 96.3 and $[\alpha]_D = +132.5°$. A number of osazones were prepared, which showed well-defined crystals of maltosazone and some glucosazone. A few crystals similar to those which Ling and Nanji considered to be *iso*maltosazone were also seen, but these did not occur consistently. The waxy conversion liquid, therefore, contains principally maltose together with small amounts of glucose and dextrins. The latter substances probably account for the fact that the reducing power is below 100 and the rotatory power of the liquid is less than that expected for a solution of pure maltose ($[\alpha]_D = +138°$).

It may be concluded from these findings that the β-amylose portions of the waxy and non-waxy starches are alike in forming maltose on hydrolysis with amylase.

α-amylose fractions of the non-waxy and waxy starches

The α-amylose portion of non-waxy maize starch, precipitated from the barley diastase conversion liquid by 60 per cent alcohol, is obtained as a firm, non-adhesive, non-elastic, white mass sparingly soluble in water. It showed the following constants: R = 13.2 and $[\alpha]_D = +255°$. A sample was treated with an active preparation of malt amylase at 50°C for 96 hours. During this period the hemicellulose separates out as a flocculent precipitate and may be filtered off. The constants on the solution at the end of the conversion period were: R = 104.6 and $[\alpha]_D = +138.1°$. Several osazones were prepared, which on recrystallization were invariably found to contain an insoluble residue, although no precipitate formed during heating. The recrystallized material showed maltosazone and a small amount of glucosazone but no *iso*maltosazone appeared to be present.

The α-amylose fraction obtained from waxy starch is markedly different in its physical properties from the corresponding substance from common maize starch. Whereas the latter is firm, crumbly and difficultly soluble in water, the waxy α-amylose is elastic, sticky and easily dissolved in water at ordinary temperatures. The constants shown were R = 12.6 and $[\alpha]_D = +167°$. While the determination of specific rotation on material of this sort is subject to rather large error on account of the effect of the methods of clearing and filtering, it seems reasonably certain that the optical properties of the waxy and non-waxy α-amyloses are significantly different. What this means, however, is not apparent. The reducing power of the α-amylose is probably due to the liberation of reducing groups in the substance itself by the alkaline iodine solution used in measuring this property. When the fresh α-amylose is treated with active beer yeast no fermentation ensues, showing that neither maltose nor glucose is present.

After 90 hours' conversion with active malt amylase the waxy α-amylose solution gave the constants R = 100.2 and $[\alpha]_D = +133°$. The crystals formed in the osazone test were rather ill-defined in appearance. Some of them simulated those of the *iso*maltosazone of Ling and Nanji (1923). After careful recrystallization, however, a clear test for maltose was obtained with no other type of crystals present. On inoculating a sample of the conversion liquid with beer yeast a vigorous fermentation developed. According to Ling and Nanji (1923) *iso*maltose is not fermentable with yeast, whereas maltose, as is well known, is readily attacked.

These experiments show that the waxy and non-waxy starches are alike in forming maltose on hydrolysis with amylase. The two fractions, α-amylose and β-amylose, examined separately by treating the starch paste first with the amylase of ungerminated barley and subsequently with malt amylase, give the same result. Traces of glucose are found in the conversion liquids and some dextrins are present. The two kinds of starch, however, show no consistent difference in this respect. The experiments afford satisfactory evidence that waxy starch, like common maize starch, is split into maltose, the yield of this sugar closely approaching the theoretical.

This conclusion is of particular interest from the genetic point of view in showing that the starches formed under the action of the waxy and non-waxy genes are alike with respect to the ultimate sugar unit of which they are composed.

Rate of hydrolysis with malt amylase

On diastatic hydrolysis the waxy and common maize starches both produce maltose, showing that they are composed of the same sugar residue. Possibly the essential difference between the two carbohydrates lies in the manner in which the sugar residues are united in the starch molecules. If this is the case one might expect that on treatment with a given amylase preparation the starches would be hydrolyzed at different rates.

In a series of tests (Brink, 1928) designed to measure the comparative rates of maltose formation, highly purified samples of waxy and non-waxy starch prepared in the laboratory were treated with malt amylase under comparable conditions of concentration and temperature. Two preparations of malt amylase were used. The first, employed in only one test, was of comparatively low diastatic power; the other, used in eight experiments, possessed a relatively high activity. The acidity of the starch pastes was adjusted with acetic acid to pH 4.5. In the samples taken for analysis, the amylase was inactivated by boiling and the reducing power determined by the iodimetric method of Baker and Hulton (1920).

In seven of the nine tests maltose was formed more rapidly from the common maize starch than from the waxy starch. In the two remaining trials there was no certain difference in either direction. In one of the tests terminated at 10 hours, where the conditions were favorable for rapid conversion, the difference in rate in favor of the common starch was maintained to the end of the experiment, when the digestion was about 90 per cent complete.

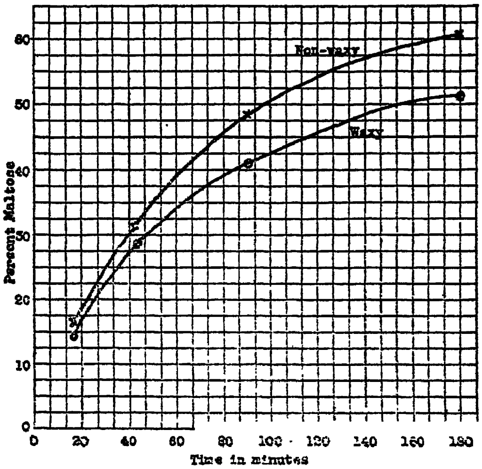

FIG. 1. RATE OF MALTOSE FORMATION FROM THE WAXY AND NON-WAXY STARCHES WHEN TREATED WITH A COMMON ENZYME, MALT AMYLASE. AVERAGE OF RESULTS IN TESTS 7, 8 AND 9

The results of the three tests, numbers 7, 8, and 9, which were carried out with the greatest degree of refinement are given in Table 3 and shown graphically in Figure 1.

The evidence afforded by these experiments clearly favors the conclusion that malt amylase hydrolyses common maize starch to maltose slightly more rapidly than it does waxy starch. This affords some justification for thinking that there is a structural difference in the molecules of the two carbohydrates.

During the conversion to maltose with malt amylase, waxy starch forms intermediate products of a lower specific rotatory power than does common maize starch. This is shown in Figure 2. If the optically active substances in the conversion liquids are identical in nature, waxy and non-waxy samples containing the same percentages of maltose should have the same specific rotation. It is seen from the figure, however, that the values for common starch stand about 14° higher than those for waxy starch when comparison is made between solutions containing the same amounts of maltose. This means that the intermediate compounds between the initial polysaccharide and the sugar are different in the waxy and non-waxy conversion liquids. If it could be assumed that dissociation of the starch is completed in the initial stages of conversion the difference in optical activity of the solutions might be taken as evidence of a structural dissimilarity in the elementary molecules. It is more likely, however, that dissociation and hydrolysis proceed side by side under the action of the enzyme. If this is the situation, the difference in specific rotation of the respective solutions may be due either to a difference in the simple molecules themselves or to the degree in which the latter are released from some unit of higher order, or to the combined effect of both.

TABLE 3

Comparative amounts of maltose formed from common maize starch and waxy maize starch under the action of a given preparation of malt amylase. The values are percentages of maltose reckoned on initial amount of moisture-free starch

		TIME IN MINUTES			
		15	45	120	180
Test 7	Common starch........	13.2	28.4	45.6	59.2
	Waxy starch...........	13.2	22.8	32.7	42.8
Test 8	Common starch........	20.9	36.9	52.8	63.3
	Waxy starch...........	18.4	34.5	48.3	58.1
Test 9	Common starch........	14.9	29.9	46.4	61.2
	Waxy starch...........	11.9	28.5	42.4	54.2
Average	Common starch....	16.3	31.7	48.3	61.2
	Waxy starch.......	14.5	28.6	41.1	51.7

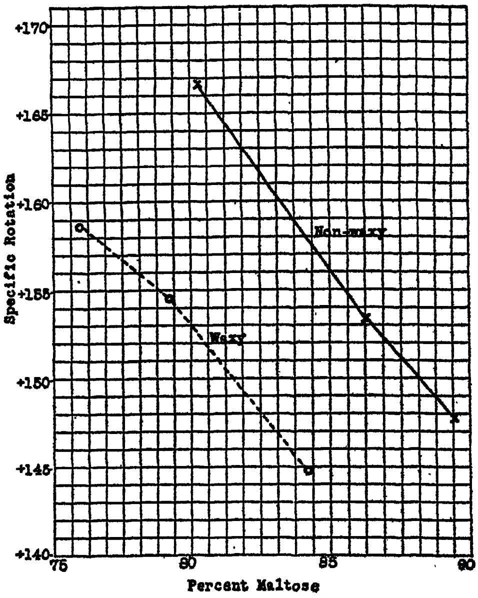

FIG. 2. SPECIFIC ROTATIONS OF THE CONVERSION LIQUIDS DURING HYDROLYSIS OF THE WAXY AND NON-WAXY STARCHES WITH MALT AMYLASE

Phosphorus content of waxy starch

Starch contains a small amount of phosphorus, which is not removed by strong acids and bases. Samec (1914) believes that the substance is present in organic combination. It is an interesting fact, the significance of which, however, is not yet known, that waxy starch contains only about one-twelfth as much phosphorus as common maize starch. Duplicate determinations (Brink, 1928) gave 0.0192 and 0.0194 per cent for common maize starch and 0.0016 and 0.0015 per cent for waxy starch. The low content of phosphorus in the waxy starch is not due to a deficiency of this element in the endosperm tissue. Endosperm meal from non-waxy seeds was found to have 0.0519 per cent P whereas comparable waxy endosperm meal contained 0.0507 per cent. While the endosperms of waxy and non-waxy maize contain practically equal amounts of phosphorus, only a minute amount is combined with the former type of starch.

Effect of the waxy gene on amylase production

With evidence at hand for a structural difference in waxy starch the next logical step was a search for the agency by which this change is effected. The first possibility to be explored was that the enzyme concerned in starch synthesis and hydrolysis, namely, amylase, formed under the action of the waxy gene was different from that produced in non-waxy plants. Enzymes have often been suggested as the means by which genes exert their differential influences, but few attempts at experimental verification have been reported. So far as the writer is aware, Onslow (1915) is the only one heretofore who has demonstrated a positive relationship between the production of an enzyme and the presence of a particular gene. He found that chloroform water extracts of the skins of recessive white and yellow rabbits lack tyrosinase, whereas similar preparations from black, chocolate and blue skins contain it.

In the present investigation (Brink, 1929) the enzymatic activity of comparable samples of waxy and non-waxy seeds, seedlings and pollen has been tested. A special effort was made to arrange the conditions of the experiments as simply as possible. To avoid the danger of modifying the activity of the preparations no attempts at purification of the enzymes were undertaken. The dried seedlings, seed and pollen were thoroughly ground, treated with water and the crude extracts tested directly on substrates of three kinds, potato, waxy maize and non-waxy maize starch pastes. The reducing power of the conversion liquids was taken as the measure of hydrolytic activity.

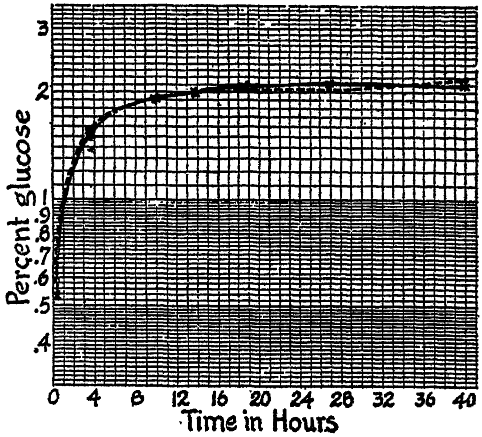

Fig. 3. Rate of Glucose Formation from Potato Starch Paste under the Action of Amylase Extracts of Waxy and Non-waxy Seedlings in Test 1

Broken line, waxy; solid line, non-waxy

Amylase of waxy and non-waxy seedlings

The waxy and non-waxy seeds on a number of segregating ears were separated and germinated on moist paper. Growth was stopped by drying at 40°C. when the radicles were about one-quarter inch in length. The dried material was finely ground and extracted with water for at least 15 hours. After straining through cheese cloth the diastatic activities of measured amounts of the extracts were tested under appropriate conditions on potato starch paste. Since the material was not treated with alcohol, maltase was associated with the amylase, producing, as the ultimate product of hydrolysis, glucose rather than maltose. The reducing powers of the conversion liquids were accordingly calculated in terms of the former sugar.

The results of a typical experiment are shown in Table 4 and plotted in Figure 3 using the arith-log scale. On this ruling the same percentage difference is always represented by the same vertical distance so that direct comparison of the rates of hydrolysis may be made. It will be observed that the waxy and non-waxy curves practically coincide throughout the 40 hour period during which the conversion was followed. This relation was corroborated in a subsequent test. It may be concluded, therefore, that in their diastatic activity the extracts of waxy and non-waxy seedlings are equal.

TABLE 4

Amounts of glucose formed on treating potato starch paste with amylase extracts from ground non-waxy and waxy seedlings respectively. Test 1

TIME	PERCENTAGE GLUCOSE IN SOLUTION	
	Non-waxy extract	Waxy extract
15 minutes	0.53	0.59
48 minutes	0.86	0.90
3.5 hours	1.57	1.58
6 hours	1.72	1.74
10 hours	1.89	1.90
14 hours	2.00	2.00
19 hours	2.07	2.07
27 hours	2.13	2.08
40 hours	2.12	2.18

It is not surprising, in view of the fact that the waxy gene does not exert a differential effect on the starch found in the embryo, that the enzyme extracts of waxy and non-waxy seedlings are equally potent. Both kinds of seedlings are rich in amylase, which appears to be secreted by cells of the embryo adjacent to the endosperm. These same cells, whether *Wx wx* or *wx wx* in composition, during the early development of the seedling lay down an abundance of starch which stains blue with iodine. It appears, therefore, that the waxy gene does not affect the starch formed in this region nor the amylase accompanying it.

THE AMYLASE OF WAXY AND NON-WAXY SEEDS

The dry mature endosperm of the corn seed contains a small amount of amylase. This, presumably, is the residue of the enzyme formed during development of the tissue. It was thought that a study of the diastatic activity of waxy and non-waxy endosperms might throw light on the influence of the waxy gene on the amylase earlier concerned in starch synthesis.

Tests with the mature seed can provide valid evidence on the enzymatic relations prevailing in the two classes of endosperms during the period of starch synthesis only if no differential inactivation of the residual amylase occurs during ripening and storage. Abegg (1929) has obtained evidence which shows that important secondary changes in the fatty substances of the endosperm do occur at these periods. These modifications are of such a nature that it seems very doubtful whether the results of tests on diastatic activity of seeds several months old afford a true picture of the difference which obtains at the time the starch is being laid down. A number of experiments were made with the amylases extracted from mature seeds and a consistently higher hydrolytic activity found in the waxy preparations (Brink, 1928). In view of the above considerations, however, these can not be accorded much significance.

Abegg's investigations show that corresponding changes do not occur in the pollen grains. On the basis of the facts at hand, therefore, the pollen provides a much more dependable source of material for studying this phase of the problem.

THE AMYLASE OF WAXY AND NON-WAXY POLLEN

Pollen is the material *par excellence* for a study of the action of the waxy gene on amylase production. The pollen grain is a simple, undifferentiated structure which becomes entirely cut off from the parent sporophyte by a heavy wall. The deposition of starch appears to continue until a few days prior to anthesis, so that the enzymes concerned in the process are probably little altered in pollen collected at this time. Maize pollen is readily killed by drying and may be preserved in a thoroughly desiccated condition over calcium chloride for a long period of time without undergoing appreciable change. In pollen taken promptly at the time of shedding and preserved in the non-living condition there would seem to be little opportunity for subsidiary reactions which would significantly alter the character of the amylase formed during starch synthesis.

The absolute amount of amylase in maize pollen is small. In order to obtain a satisfactory measure of its activity it is necessary to prolong the conversions to at least 48 hours and double this time is preferable. In the early stages of hydrolysis the conversion liquid is rather turbid so that small differences can not be accurately established in titration. Later, however, the solutions are clear.

Three tests were made with samples of pollen from closely related waxy and non-waxy plants. The dry pollen was reduced to a fine powder by 36 hours grinding in a ball mill and treated with water over night in the presence of a little toluol to check fermentation. The mixture of powdered pollen and water was then added directly to the starch paste and the amount of glucose formed was measured by the iodimetric method of Baker and Hulton in samples taken at intervals.

In each of the experiments made, the non-waxy pollen showed a higher diastatic power than the waxy. There is a little uncertainty attaching to the differences in rate at the earliest stages, due to the turbidity of the solutions, but as soon as clear readings become possible, larger amounts of glucose are always found in the non-waxy samples.

The results of a typical test (Brink, 1929) carried to 125 hours, with waxy maize starch paste as the substrate, are shown in Table 5 and figure 4. It will be noted that the rate from about five hours onward is clearly higher in the non-waxy than in the waxy lot.

TABLE 5

Amounts of glucose formed from waxy maize starch paste under the action of Su Wx and Su wx pollen extracts. Test 15

TIME IN HOURS	PER CENT GLUCOSE ON STARCH	
	Non-waxy extract	Waxy extract
1	16.57	17.72
9	20.03	19.31
25	24.50	21.32
50	28.82	22.19
75	31.85	23.35
100	35.45	24.64
125	39.20	25.79

As pointed out earlier in the paper, heterozygous waxy plants homozygous for the sugary gene (*su su Wx wx*) give significantly lower waxy ratios when used as pollen parents than do individuals carrying the non-sugary factor. This is attributed to some indirect effect exerted by the sugary gene on the microspores through the parent sporophyte which increases the handicap upon the waxy pollen tubes during the first stage of growth. An effort was made to determine whether the exaggerating effect of the sugary gene on the waxy:non-waxy ratio is reflected in the diastatic activity of the two sorts of pollen.

The results of three tests on comparable samples of *su Wx* and *su wx* pollen show a consistently higher rate of hydrolysis in the case of the non-waxy pollen but the difference does not appear to be any greater than that for the corresponding classes of non-sugary pollen.

3. On Harrison's view the violet reaction (reddish-brown by reflected light) given by waxy starch paste on treatment with iodine indicates that the particles of which this carbohydrate is composed are smaller than those of common starch. The forces responsible for binding the elementary molecules of starch into units of a higher order, a phenomenon known as association, are not understood. It would appear, however, that the waxy gene exerts an influence on them.

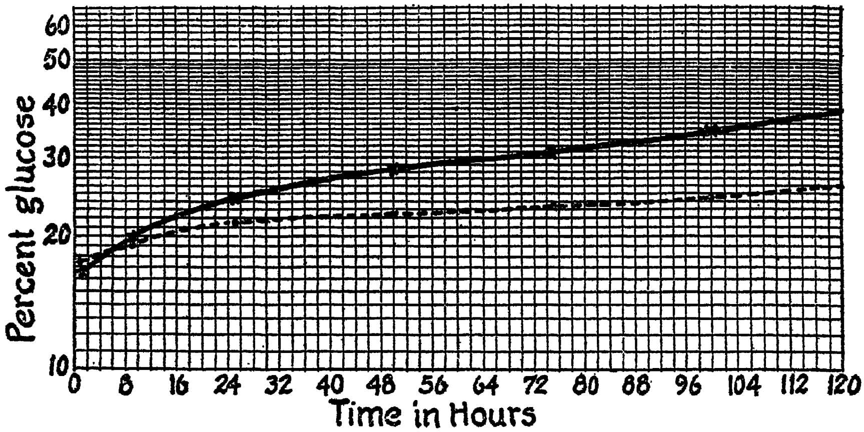

FIG. 4. RATE OF GLUCOSE FORMATION FROM WAXY MAIZE STARCH PASTE UNDER THE ACTION OF AMYLASE EXTRACTS FROM *Su Wx* AND *Su wx* POLLEN

Broken line, waxy; solid line, non-waxy

Summary of the biochemical effects of the waxy gene

1. The carbohydrate stored in the endosperm of waxy seeds when isolated in pure condition is found to be organized in granular form very similar to that of common maize starch.

2. Proximate analyses of non-waxy and waxy seed and pollen show that the principal carbohydrate in both is starch. Very little dextrin is present in either. On the basis of its insolubility in water and in 10 per cent alcohol, the peculiar carbohydrate formed by waxy plants is to be considered a starch rather than a dextrin.

4. When measured by the centrifugation method of Sherman and Baker, waxy starch is found to contain a considerably higher proportion of β-amylose than common starch. The barley diastase method of Ling and Nanji, on the other hand, indicates that the amount of this constituent is nearly the same in the two kinds of starch grains. The discrepancy in the results may be explained on the assumption that the waxy particles are smaller than those of non-waxy starch and consequently behave differently in the centrifuge.

5. Waxy starch contains only a trace of hemicellulose as opposed to 3.6 per cent

reported by Schryver and Thomas for ordinary maize starch.

6. Waxy starch, like the non-waxy sort, forms a single sugar, maltose, on hydrolysis with malt amylase. This shows that the two substances are composed of the same building stones and that the waxy gene exerts its differential effect subsequent to the sugar stage in the formation of starch.

7. Under the action of a given preparation of malt amylase, waxy starch is converted to sugar somewhat more slowly than the non-waxy starch. In explanation of this it is suggested that the maltose residues in waxy starch are linked together in a way slightly different from that in common starch.

8. Waxy starch contains about one-twelfth the amount of organic phosphorus present in the non-waxy sort.

9. Aqueous extracts of waxy and non-waxy seedlings show equal diastatic activity when tested on potato starch paste substrates. Since most of the enzyme contained in the seedlings is produced by cells of the embryo which form blue-staining starch grains in waxy as well as non-waxy seeds, a difference in amylase activity of the seedling extracts is not to be expected.

10. Similar extracts from the two classes of pollen show a consistently higher diastatic activity in the case of the non-waxy type. The difference is displayed on substrates of waxy or non-waxy maize starch and potato starch paste. This fact indicates that the primary effect of the waxy gene may be upon the enzyme amylase.

DISCUSSION

The waxy condition in maize is almost unique among Mendelian characters in the flowering plants in affording an opportunity for studying the physiology of a gene in the haploid generation. In microspore and macrospore, the gene manifests its action immediately following the reduction divisions. The pollen grains and embryo sacs receiving the non-waxy factor lay down common starch as the chief carbohydrate reserve; those to which the waxy gene is transmitted manufacture a different type of starch from the same kind of materials contributed by the parent sporophyte. In what way is the waxy starch unlike the common sort and what is the nature of the change in the mechanism of starch synthesis that leads to the new product?

The problem would be simpler if starch were a substance more amenable to structural analysis. Thus far chemists have been unable to agree on the constitution of this polysaccharide, although it has long been known that it is built up of glucose residues. The number of glucose units in the starch molecule and the way in which they are united, however, are still open questions. Possibly the methods which have proved so effective in revealing the structure of the sugars will be of much more limited value in dealing with this more complex carbohydrate which exhibits colloidal properties. At the present time less direct methods of approach, such as the use of enzymes as exploring agents, hold greater promise of advance.

The present studies make it clear that the difference in the waxy and non-waxy reserve products is primarily in the starches themselves and not in the sugar unit which enters into their formation. Both the waxy and non-waxy starches are split into the same sugar, maltose, on diastatic hydrolysis. The fact that the reaction proceeds at a slightly different rate in the two cases suggests a difference in structure of the starch molecules which puts the one class slightly out of adjustment with the enzyme. As to what the actual change in structure is, the experiments afford no information.

The possibility is not excluded by any of the results obtained that the fundamental molecules of the waxy and non-waxy starches are structurally alike and that the carbohydrates differ in the degree to which their simple units are "associated" or bound together by forces other than chemical valency. In fact the difference in color reaction with iodine and the dissimilar behavior of the starch pastes on centrifugation strongly suggest that the particles of waxy starch are actually smaller than those of the other type. This might be a secondary result, however, of some fundamental difference in the elementary molecules themselves.

The lower diastatic activity of the waxy pollen as compared with that of the non-waxy type is suggestive of the agency by which the waxy gene exerts its effect on the kind of starch formed. The amylases in the two classes of pollen differ either in kind or amount. In view of the catalytic nature of the substances and the fact that the difference in the end-products is a qualitative and not a quantitative one, the former is the more likely. It may be assumed that the immediate effect of the waxy gene is the production of an amylase, slightly different in nature from that formed under the action of the allelomorphic non-waxy factor. The waxy amylase promotes the union of the sugar molecules in starch formation in an abnormal way.

The lower diastatic activity of waxy pollen is in conformity with the facts on pollen-tube growth. In matings of the types *wx wx* ♀ × *Wx wx* ♂ and *Wx wx* selfed, the proportion of waxy seeds is usually slightly in defect of that expected on the Mendelian basis. This deficiency might well follow from a slower development of the waxy pollen tubes due to less rapid hydrolysis of their starch reserves.

A comparison of the mode of action of the waxy and the sugary genes on pollen tubes growth affords some insight into the manner in which the waxy factor probably operates. The sugary gene differentially affects the growth of waxy and non-waxy pollen tubes but only when present in homozygous condition in the parent sporophyte. In other words, *su Wx* and *su wx* male gametophytes arising from *su su Wx wx* plants show a marked difference in ability to effect fertilization whereas the same two classes of pollen from *Su su Wx wx* individuals develop at nearly equal rates. Evidently it is the effect of the sugary factor on the parent diploid plant which counts. The waxy gene, on the other hand, calls forth an immediate response in the pollen as soon as it is segregated from its dominant allelomorph. In contrast to the sugary factor it acts in a direct way. Such a prompt effect is suggestive of an influence on some catalytic agency. The physiological action of the waxy gene seems most intelligible on the assumption that the gene controls the formation of the enzyme amylase which functions directly in starch synthesis.

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THE DETERMINATION OF THE NEURAL PLATE IN URODELES

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PROMORPHOLOGY OF THE URODELE

AN AMPHIBIAN egg when first laid shows but little complexity of structure compared with that of the larva which shortly develops from it. It displays polarity in that one half of the egg is less dense than the other half; and, since the egg soon after laying lies free in its membranes, this lighter half rotates to the top. The upper hemisphere is also darkly pigmented superficially. Internally polarity reveals itself in an increase in the size and concentration of yolk granules from the upper or animal pole to the lower or vegetal pole. The nucleus lies nearer the animal pole.

Careful examination discovers a bilateral as well as a polarized structure in some urodele eggs. The egg of our Pacific newt, *Triturus torosus*, floats with the center of the pigmented area not exactly at the top. A crescent of white is thus to be seen when the egg is viewed directly from above, and in some specimens this crescent is actually of more brilliant lustre than the remainder of the non-pigmented area. Vogt (1926a) describes such a condition in *Amblystoma tigrinum* and in *Pleurodeles*. In other urodeles, the Tritons, for example, such visible evidences of bilaterality are not readily discerned, but experiment has clearly shown that even in such cases the future fates of the two sides are distinguished. Bánki (1928) studied the white crescent of *Amblystoma* and found that it originates in a descent of protoplasm on one side of the egg from beneath the pigment of the animal area. This movement of protoplasm pushes the yolk granules of the vegetal area before it; and the shift in the position of the center of gravity which thus results causes the egg axis to take an oblique direction. Evidence of such a movement of protoplasm in the egg of *Triturus* is occasionally seen in streaks of pigment, torn from the margin of the animal area, which cross the white crescent in a meridional direction. Morgan (1927) accounts for the gray crescent in the frog's egg by a similar movement of substance. Bánki finds some indication of bilaterality in *Amblystoma* even before fertilization has taken place.

Such is the extent of the visible differentiation of the urodele egg when first laid; and throughout the period of segmentation into many cells there is but little increase in observable diversity. The cells of the animal hemisphere are smaller than those of the vegetal hemisphere, and the cleavage cavity which forms within the ball of cells lies nearer the animal pole; but the chemical differentiations which all the while are undoubtedly taking place cannot be visibly demonstrated.

Now, it has been possible by several methods, notably by marking the surface of the developing eggs with vital dyes, to trace the continuity of materials through the foldings and moldings which follow segmentation, and by reasoning backward to make a map of the surface of the blastula indicating the regions which give origin ultimately to this or to that structure of the embryo. Areas thus distinguished by their future rather than by their present visible diversity have been called *prospective organ rudiments.* Thus we shall refer to the region which becomes the neural plate as *prospective neural plate material.*

Figure 1, taken from Vogt (1926b, 1929) is a schematic charting of the prospective rudiments of the urodele egg at the beginning of gastrulation. The arrow points to the position of commencing invagination. Two transverse lines in the diagram divide the egg into three zones: (1) an upper zone of material (prospective neural plate and epidermis) which increases in area as gastrulation proceeds, until it covers the whole outer surface of the gastrula; (2) a middle zone of cells which descends and rolls beneath the lips of the blastopore, converging toward the dorsal side as it does so, to give rise to the mesoderm and chorda of the primary roof of the archenteron; and (3) a lower zone of material which will be overgrown by the blastoporal margins and become the floor and sides of the enteron—later its definitive roof as well. Roughly, the upper zone corresponds to the pigmented region of the animal hemisphere and the prospective chorda to the crescent, although the relation here is statistical rather than absolute (Bánki, 1927). In *Triturus* there is a small gray area at the vegetal pole which finally comes to occupy a position in the floor of the intestine. Minor subdivisions of the mesoderm are indicated in the figure.

DETERMINATION AS CHEMICAL DIFFERENTIATION

Such diagrams as this one which Vogt has given us bring us face to face with an issue of fundamental importance; namely, to what extent are the different areas of the blastula, prospectively this and that, also potentially the same structures? To what extent are they chemically differentiated, determined as to their fates; or are they indifferent, their determination an event of the future? In a word, are they "pre-primordia"? The experiments thus far referred to do not answer this question. They serve to trace the continuity of materials during development, but they do not tell us of causal relationships.

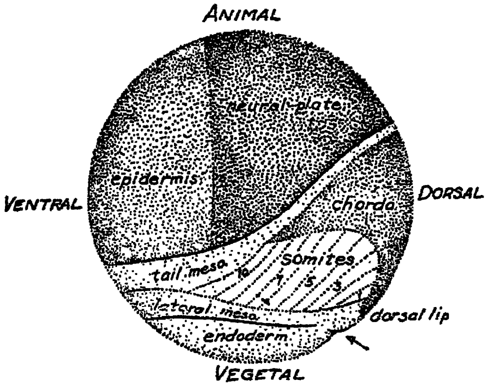

FIG. 1. PROSPECTIVE ORGAN RUDIMENTS OF EARLY GASTRULA

A schematic view of an early gastrula as seen from the left side, indicating the regions which differ according to their prospective fates. The arrow points to the beginning invagination. (Redrawn from Vogt, 1926b.)

In discussing this problem we shall find it of advantage to adopt a positive terminology. There is a negative habit of speech which pictures the progressive specialization of an egg during its development as a "localization," a progressive limitation to definite loci of potentialities already present but more widely distributed. Of this sort are the concepts of "genetic restriction" and "embryonic segregation" (Lillie, 1929). Now such language has served well, and cannot be gainsaid so long as the potentialities are thought of as purely conceptual things without objective counterpart in nature. To invest them with reality, however, and think of them as corpuscles of some sort, or as chemical stuffs, is to create abstruse problems incapable of solution. Among such are the problems of the origin, nature, and mechanism of localization of the hypothetical entities.

The positive terminology avoids these difficulties. It pictures development (at least so far as the cytoplasm is concerned) as an actual and orderly coming-into-being of diversity, a true epigenesis. First there appears chemical diversity; then, and arising by reason of the chemical diversity, structural differences. The advantage of the positive view is that it does not assume the existence at any moment of development of a greater degree of somatic complexity than can be demonstrated and experimentally investigated.

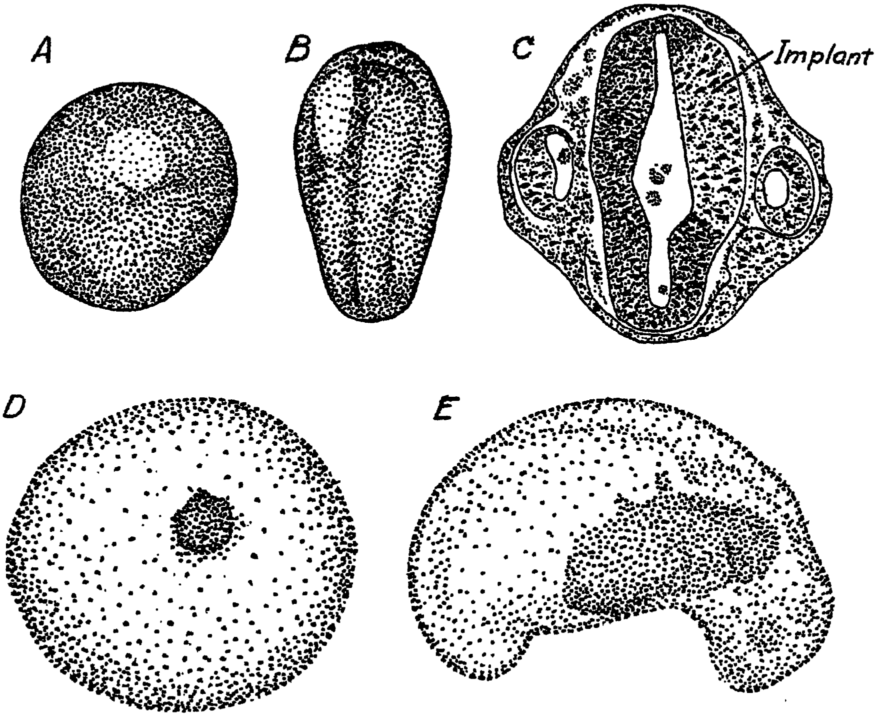

Fig. 2. "Relative Indifference" of Prospective Organ Rudiments

A. A small disc of prospective epidermis from an early *Triton cristatus* gastrula has been implanted in the prospective neural plate area of an early *T. taeniatus* gastrula. *B* and *C.* It has differentiated according to its new location into nervous tissue. *D.* In the converse experiment the disc of prospective neural plate material removed from the *T. taeniatus* gastrula has been implanted in the region of prospective epidermis of the *T. cristatus* gastrula, and (*E*) has differentiated according to its new location as epidermis. (After Spemann, 1921.)

The term now in use to describe specialization positively conceived is the word *determination*. Determination may be defined as that process of invisible presumably chemical differentiation which causally precedes the appearance of a visible organ rudiment. By reason of continued determination the egg, at first indifferent, becomes more and more a *mosaic*. A region thus actually, although as yet invisibly, set apart may be termed a *pre-primordium* or *chemical rudiment*. The central problem of this review, then, is the determination, that is to say, the chemical differentiation of the pre-primordium of the urodele central nervous sytem.

The best place to begin our discussion of experimental evidence is with the notable work of Spemann and his associates in Germany. Inasmuch as the earlier work (through 1926) has been reviewed in English by de Beer (1927), Morgan (1927), and by Spemann himself (1925, 1927), we shall not find it necessary to consider it in detail. The outstanding method of these investigations, although by no means the only method, has been that of transplanting tissue from one region of one embryo to another region of another embryo, and then noting the effect of the operation on the transplant itself and on the surrounding tissue of the host. The results may be summarized as follows:

(1) During the blastular period, and even at the beginning of gastrulation the different regions of the urodele egg are "relatively indifferent" as to their fates. If small pieces are transplanted they may differentiate according to their new locations (fig. 2). Now, as we shall presently see, this does not prove that they are undifferentiated when transplanted. It shows only that whatever chemical diversity may already be present is labile and capable of being reversed under the influence of new surroundings. (Spemann 1918, 1921; Mangold, 1923; Bytinski-Salz, 1929a.)

(2) An important exception is to be made to this principle, however; Spemann (1918) found that prospective chorda-mesoderm taken from just above the dorsal lip of the blastopore at its first appearance, and transplanted to another region of another gastrula, differentiates, not according to its new location, but according to its original location. Such material, inserted on the lateral or ventral side, produces secondary dorsal structures; namely, secondary neural tube, notochord, and somites. The experimental evidence, therefore, is that the material of the dorsal lip region is already irreversibly determined even in the late blastula; or at any rate it is determined to such an extent that it is not altered under the influence of the new surroundings in which it is placed.

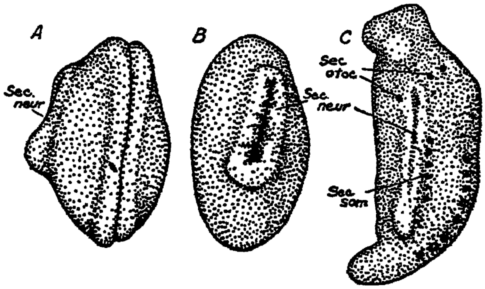

FIG. 3. "ORGANIZER" GRAFT

A disc of prospective chorda-mesoderm (organizer) from the dorsal lip of a *Triton cristatus* gastrula has been implanted on the left side of a *T. taeniatus* gastrula. *A* and *B* are dorsal and lateral views of a later stage of development, and show both the primary and the secondary neural plates. *C* is a still later stage, and shows secondary neural axis, otocysts, and somites, in addition to the structures of the primary axis. (After Spemann and Mangold, 1924.)

(3) Spemann (1918) has carried the analysis further and has shown that the prospective chorda-mesoderm of the dorsal lip acts in development as a "center of organization" in determining the chemical differentiation of the remainder of the egg. It is as though, starting from it, there was a "flow of determination" forward to other regions, notably to the region of prospective neural plate material. It is by reason of this "flow" that the latter becomes a pre-primordium. (See Spemann, 1919; Wessel, 1926.) Furthermore, if dorsal lip material be transplanted

to an indifferent region of another egg, it not only itself differentiates into dorsal structures, but it *induces* the formation of secondary neural plate substance and secondary somites from the substance of the host (fig. 3). On account of this organizing capacity, Spemann has called the material of the dorsal lip, *the organizer*. (Spemann, 1921; Spemann und H. Mangold, 1924; Geinitz, 1925.)

What now is the mode of action of the organizer, and what the nature of the flow of determination? Critical experiments by Marx (1925), Geinitz (1925), Bautzmann (1926), and Weber (1928) have shown that the "flow" is none other than the actual sinking of chorda-mesoderm beneath the surface of the egg and its migration forward to its definitive position beneath neural plate material. It appears from this that the organizing induction is a result of actual contact between chorda-mesoderm and the ectoderm which overlies it; an event analogous to the stimulus by which, at a somewhat later period in development, the contact of the optic cup induces the epidermis to differentiate a lens.

(Suzuki (1928) has shown that the capacity to "organize" nervous tissue is not confined to the chorda-mesoderm of the dorsal side, but is a general property of the entire equatorial belt. Injury to the ventral or lateral prospective mesoderm results in defects in the neural tube in the tail region.)

The picture which this work of Spemann and his students gives is that of a quite undifferentiated egg undergoing determination during gastrulation as a result of the organizing activity of the chorda-mesoderm. But this interpretation has not gone unchallenged. It has been asserted (as by Vogt, Goerttler, and Brachet) that Spemann's results reveal only secondary and "regulative" capacities of the egg, capacities akin to the power of regeneration rather than to the processes of normal development. The criticism brings us face to face with the dilemma of experimental morphology. On the one hand the mere observation of normal development cannot tell us of causal relationships. On the other hand, experimental procedures, if successful, produce abnormal conditions which can be interpreted and applied to normal development only with caution. It is always possible that experimental manipulation may have awakened properties normally in abeyance, and thus have confused the issue. I suppose a large personal element must always enter into one's interpretation of experimental results. I shall return to the significance of Spemann's results presently.

DETERMINATION AS A CONTINUED PROCESS

Recent work, much of which has been reported since the reviews of Morgan and de Beer were written, makes it certain that the differentiation of egg substance begins earlier than the experiments of Spemann and his students might lead one to expect. It has been abundantly shown that the regions of the urodele blastula are not indifferent, but are already differentiated as chemical rudiments.

Vogt (1924) and Mangold (1925) were among the first to make observations which pointed in this direction. They found that pieces of a blastula when transplanted to other regions, although capable of differentiating histologically according to their new locations, nevertheless display a tendency to perform movements typical of their first position. Prospective epidermis, transplanted to a mesodermal region, differentiates into mesodermal structures; but it tends to spread just as it would have spread had it not been transplanted. Prospective mesoderm, in a similar manner, transplanted to an ectodermal region, carries with it the tendency to invaginate and to stream. Vogt describes the phenomenon very aptly by saying that the regions of the early gastrula are already *dynamically determined* to perform their characteristic movements of gastrulation.

Goerttler (1925) has demonstrated that the material of the blastula previous to gastrulation is also *determined materially*. Instead of transplanting the tissues to new surroundings, as Spemann did, thus bringing them under the influence of changed conditions, he seared the blastoporal lip and thus prevented the normal movements of gastrulation from taking place. He found that prospective neural plate material was able to differentiate *in situ* even when not in contact with underlying chorda-mesoderm (fig. 4). The conclusion is hardly to be avoided that by the end of the blastula stage the material of the neural plate is already determined as to its fate. It is at least a labile pre-primordium.

Recently Vogt (1928b) has discussed the evidence for early determination from another angle. Emphasizing especially the work of Suzuki (1928) he notes that although a defect produced at an early stage in development may heal, and complete restitution of all parts be effected, yet there frequently remains a quantitative weakening in the size and activity of those portions of the embryo which correspond to the region injured. We have here complete qualitative restitution of primordia combined with incomplete quantitative regulation. Thus it is again evident that the blastula is a chemical mosaic.

Vogt (1927, 1928a) finds further evidence of early determination in experiments in which he retarded the development of one half of a blastula while permitting the other half to progress normally. His first method was to embed half of the egg in wax, thus cutting off the oxygen supply to the half. Later he devised a method of fitting the eggs into windows in a thin silver partition, on one side of which there flowed cold water, on the other side water at laboratory temperature. He was notably successful in obtaining the results for which he sought. The favored halves developed apparently normally, while the other halves were retarded. In his 1927 paper he records no effect of the "physiological isolation" of the half on the pattern of its differentiation. The eggs when removed continued to develop, each half with a tempo of its own. The results he terms "age-chimaerae." Later work, however, has caused Vogt to modify his first interpretation; and he now recognizes a decided influence of the environmental factors on differentiation. However, he interprets these effects as secondary and regulative. His general conclusion is that his experiments indicate a considerable amount of chemical differentiation in the cleavage and blastula stages of development which can only be secondarily upset by environmental differences.

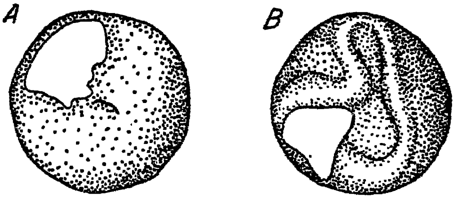

FIG. 4. DIFFERENTIATION OF NEURAL TISSUE INDEPENDENTLY OF MESODERM

A. An early gastrula of Pleurodeles was injured on the left side of the blastopore by means of a hot needle. *B.* The injury prevented the invagination of prospective mesoderm on this side; nevertheless a left neural fold developed. (After Goerttler, 1925.)

Lehmann's work (1926, 1928) bridges the gap between the results which indicate that the determination of the neural plate is early, and those which indicate that it occurs later, during gastrulation. By a method similar to Goerttler's he injured the dorsal lip of the blastopore with a hot needle at different times during the progress of gastrulation. As a result different regions of the prospective neural plate remained free from underlying chorda-mesoderm. Lehmann finds that under such conditions neural tissue may differentiate even in regions from which chorda-mesoderm is lacking. This is especially true of the region of the neural plate anterior to the otocyst. But, and here is the crucial feature of his work, he finds that the mass and arrangement of nervous tissue, the formation and closure of neural folds, the distribution of nuclei in the wall of the neural tube, and the form of the floor plate—these things are dependent in a quantitative fashion on the presence of a chorda-mesodermal substrate. Lehmann (1928) is hence led to picture the neural pre-primordium before the displacements of gastrulation have occurred as made up of two portions: a central portion (the neural centrum) located toward the anterior end of the neural plate, and a bordering zone which surrounds this and extends backward to the dorsal lip. The centrum is relatively the more completely and irreversibly determined as to its fate. It is least influenced by the lack of mesoderm beneath it. The bordering zone is relatively indifferent, becoming at its margins indistinguishable from the adjacent prospective epidermis. The rôle of the chorda-mesoderm (organizer), in Lehmann's opinion, is to complete and render irreversible the determination of the central portion, and to fix the amount and extent of the bordering zone which shall become nervous tissue. Thus Lehmann's work indicates both the reality of an early determination and the importance of the mesodermal substrate in completing the determination already begun.

Recently Lehmann (1929) by revolving pieces from the margin of the neural plate through 180 degrees, has demonstrated the progressive increase in the determination of the neural plate during the course of gastrulation, as a result of the influence of underlying chorda-mesoderm. And furthermore Mangold (1929), by inserting neural plate material of early, middle, and late gastrulae, and of neurulae into the blastocoele of host gastrulae, has shown a progressive, not a sudden increase in the degree of determination during the course of gastrulation.

There would seem to be four attitudes possible with respect to the evidence now before us. (1) We may with Spemann (see Spemann und Geinitz, 1927) recognize two stages in neural plate differentation, an early and a late. The first takes place early in cleavage, just how early has not as yet been shown. This determination is reversible and incomplete. The second occurs during gastrulation and serves to stabilize and complete what has already been begun. Thus we have here, as elsewhere in development, evidence of a "double assurance" that development shall be orderly and the product of development an adaptive organism. Spemann suggests that both determinations of neural plate material may take place in relation to the chorda-mesoderm; the first as a result of proximity to chorda-mesoderm, the second in consequence of actual contact.

(2) Or we may with Lillie (1929) discount the evidence of an early, labile determination. "There is no doubt that germinal areas possess specific *qualities* at all stages, and that certain of these are essential means of embryonic development;" but this, Lillie believes, does not amount to a determination ("embryonic segregation"). He thinks of determination as a "single decisive event," occupying a very brief interval of time.

(3) Or we may with Vogt, Goerttler, and Brachet stress early determination and interpret Spemann's results as indicative of secondary capacities of the egg, capacities related to regeneration. Not that the early determination is necessarily a complete determination, for it is not; rather it is, to use Vogt's term, a *Bahnung* or preparing of the way for further development. The organization present in the very young egg guarantees the orderly course of later determination. Later development is, as it were, a filling-in of detail.

(4) Neither of these interpretations appeals as quite satisfactory. The concept of "double assurance" conflicts with one's sense of the economy of nature, as does also the assertion that secondary properties exist in the egg. May we not interpret the evidence in terms of a single, long-drawn-out process of determination? The determination of neural plate material begins early in cleavage, if not earlier. It continues with ever increasing definiteness (Lehmann, 1929; Mangold, 1929) as gastrulation progresses, yes, perhaps until the visible rudiment has begun to appear. According to such a concept the early blastula is not indifferent; it is already a chemical mosaic. On this basis it is easy to appreciate that at first determination should be labile and should gradually attain a condition of irreversibility. The early determination, furthermore, is incomplete in that of itself it cannot produce a neural plate of normal mass and structure. We may think of regulation (in developing eggs) as a property related to normal development. It reflects the very mechanism of differentiation. Just as evidence of a mosaic pattern indicates that determination has begun, so the capacity for regulation reveals that determination is still in progress. The importance of the capacity is that it supplies *sustained assurance* throughout the long process of chemical diversification that the final outcome shall be orderly. In the words of Lillie (1927): "The possibility of normal development depends among other things upon flexible but finally precise adjustments of localization (determination) of specific parts everywhere in the embryo."

THE PHYSIOLOGICAL PATTERN OF THE URODELE EGG

The experiments which we have reviewed thus far afford a partial solution of the problem of neural plate determination. They tell us of the time of determination, and something of the conditions under which it takes place; but they do not reveal in any clear fashion the nature of the inducing stimulus. Are we to think of the stimulus as specific, some chemical hormone perhaps; or are we to picture it as non-specific and quantitative, some amount of substance, rate of activity, or oxidative potential, which operates by releasing capacities inherent in the material stimulated? The time is not ripe for an extended discussion of the question. There are lines of evidence, however, mostly of recent date, which indicate that the inducing stimulus is indeed of a non-specific and quantitative nature.

In his Croonian lecture, Spemann (1927) presents evidence that the material of the dorsal lip possesses "longitudinal structure"; also bilateral structure or "laterality." A secondary embryo induced by an implant need not have exactly the same orientation as the primary. In one instance, for example, secondary ear-vesicles formed symmetrically to the right and left of the induced neural plate to which they were related, but they were one behind the other in relation to the axis of the host. Spemann concludes that the organizer must have "some longitudinal structure, which is not lost by transplantation and which determines the direction of its invagination and consequently of induction." There are limits, however, to the possible lack of harmony between the primary and secondary axes, as Bautzmann (1928a) has clearly shown. Embryonic axes oriented in opposite directions have not been obtained; and there is, moreover, a decided tendency for primary and secondary organs of the same nature, for example, otocysts, to differentiate at the same level with respect to the long axis of the egg as a whole. This in itself indicates longitudinal structure. (De Beer, 1927.)

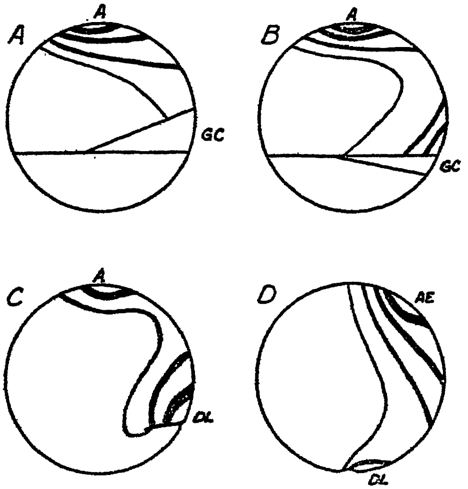

Fig. 5. The Pattern of Susceptibility in the Developing Frog's Egg

A. In the unsegmented egg disintegration begins at the animal pole but spreads most rapidly toward the grey crescent. *B.* In the many-celled blastula disintegration also begins at the animal pole; but a secondary center soon appears at the future dorsal lip of the blastopore. *C.* Disintegration in the early gastrula begins at the dorsal lip; later at the animal pole. *D.* In the early neurula disintegration begins at the anterior end of the developing neural axis. (*A*, *B*, and *C* are based on figures by Bellamy, 1919. *D* is drawn from descriptions by the same author.)

Goerttler (1927) has attempted an experimental analysis of the axiate pattern of the entire egg. Employing a modified form of Spemann's technique he has transplanted quadrangles of tissue from one embryo to another, keeping note always of the orientation of the transplant. He found that pieces of prospective neural plate material of early gastrulae, implanted into the ventral abdominal wall of stages as late as early neurulae, differentiate as small neural plates. But they do this only provided that they were placed in harmonious orientation to the substance of the host; that is, provided they were placed in such position that their dynamic activities in gastrulation and neurulation are unhindered. The experiments clearly indicate the presence of a longitudinal and directional organization.

A further observation of Goerttler's shows bilateral structure in the region of the organizer. Quadrangles from the left side of the blastoporal lip, implanted on the right side of eggs of similar age, invaginated in accord with their dynamic potentialities and contributed to the mesoderm of the host. They also induced secondary neural structures; but, and this is the important feature, the secondary structures were partial, being of left orientation. Thus neurulae were produced possessing two left neural folds but only one right neural fold.

These experiments lead to a concept of the parts of the blastula as possessing an organization which is quantitative and directional. Goerttler pictures the formative forces as strongest and most numerous in the vicinity of the dorsal lip of the blastopore, and as radiating out from there with decreasing vigor to other parts of the egg. The activity and fate of an implant, according to his evidence, depend upon the relation between the dynamic pattern which it brings with it and the pattern of the field into which it is placed.

Such a dynamic pattern, involving as it does longitudinal and bilateral structure, requires to be visualized in physiological terms. The most available concept to this end would seem to be the hypothesis of physiological gradients as advanced by Child (1921, 1925, 1929). In relation to the present problem the hypothesis involves two main propositions: (1) that the developing egg possesses a physiological pattern or configuration in which different regions differ quantitatively in their relative rates of "metabolic" activity; and (2) that the morphogenic changes which go on in such eggs are related to the physiological pattern. As I see it, the essential feature is not that function precedes structure, but that quantitative differences expressing themselves functionally issue in qualitative differences.

Bellamy (1919) published a paper in which he sought to analyse the functional pattern of the frog's egg at early stages in its development by the method of observing the relative susceptibilities of the different regions to toxic agents. He showed that in this egg, as in organisms generally, the regions of greatest activity are the first to disintegrate when exposed to lethal concentrations of a variety of substances, or to extreme cold. The unsegmented egg begins to disintegrate first at the animal pole, the disintegration spreading most rapidly along the dorsal surface toward the gray crescent or region of the organizer (fig. 5A). In the many-celled blastula disintegration also begins at the animal pole, but there is now a new region of high susceptibility just above the gray crescent in the region which shortly gives rise to the dorsal lip of the blastopore (fig. 5B). With the onset of gastrulation this second region increases in sensitivity; while at the same time the area of susceptibility of the animal pole diminishes (fig. 5C). The condition continues throughout the formation and closure of the blastopore. Just before the neural folds become visible, however, a third region of high susceptibility (Bellamy would identify it with the first) makes its appearance at what will shortly become the anterior end of the neural axis (center of brain area) (Fig. 5D).

These experiments reveal a physiological pattern which is kaleidoscopic, shifting here and there during development as now this region and now that region enters into increased developmental activity. (a) The animal pole is the dominant area before and during the early cleavages of the egg. May we not conceive of it as the high end of the primary gradient in relation to which the materials of the three primary zones of the egg, prospective ectoderm, prospective chorda-mesoderm, and prospective entoderm are first (although as yet reversibly) established? Child (1929) would hold that it also organizes by induction the anterior region of the embryo. The difficulty here is that the animal pole becomes apparently a point of no definite significance in the later development of the embryo (see Kingsbury, 1926). It gives rise to a region of the brain in most urodeles, but to a point in the ventral epidermis in anurans (Brachet, 1927). (b) Physiological dominance now passes to the region of the dorsal lip, which is early established and which soon becomes dynamically the most active region of the egg. It is no doubt in relation to the field of activity of this area that the early, labile chemical differentiation of neural plate material—and no doubt of other materials of the egg as well—is determined. De Beer has expressed this idea in his 1927 review: "There is strong support for the view that the various rudiments become determined at certain levels in a gradient co-ordinate system of which the abscissa culminates at the organizer and the ordinate at the animal pole." I would only change this by suggesting that a given area is under the influence of the animal pole *before* it comes under the influence of the organizer. How can a region be under the dominance of two centers at one time? The dorsal lip persists for some time as the actively growing tail bud. (c) The third center of metabolic activity at the anterior end of the neural groove is apparently to be correlated with the central area of the neural pre-primordium described by Lehmann (1928). May we not think of it as the dominant region in relation to which the floor, basal, alar, and neural crest areas of the neural plate are established (Kingsbury, 1922)?

EXPERIMENTS WITH THERMAL GRADIENTS

More direct, although as yet not extensive evidence, of the relation between the physiological pattern and the differentiation of the neural plate, is to be found in thermal gradient experiments. Huxley (1927) compressed frog's eggs lightly between two chambers containing water at different degrees of temperature. The eggs were left in their jellies and were surrounded, except where in contact with the walls of the chambers, with humid air. He found, among other results, that warming the upper pole (gradient, "adjuvant") produced a relatively large head; while warming the lower pole (gradient, "antagonistic") produced a relatively large body. Dean, Shaw, and Tazelaar (1928), working in Huxley's laboratory, have continued and extended his studies and have added notes on the effects of transverse temperature gradients; also on the effect of temperature differentials applied to the gastrula and later stages. They record striking asymmetry in the development of the lateral neural folds and mesoderm when one side is warmed. They note further that to a considerable extent, eggs which have been radically upset in the time-relations of their development are able to straighten themselves out and produce forms that are quite normal. Nevertheless, it is certain on the basis of their results, that artificially speeding up the metabolic activity of a part of the neural pre-primordium does actually increase the amount of material which differentiates to form neural tissue. "It would seem that there may exist a 'critical point' as regards the amount of asymmetry capable of regulation."

By a method quite different from that of Huxley, I have (1928) applied temperature differentials to the eggs of the Pacific Coast urodele, *Triturus torosus*. It occurred to me, as it did to Huxley, that if I could modify the physiological pattern by such a gradient, at a definite time and in a definite manner, I should be able to control the invisible differentiation of pre-primordia and affect the formation of visible rudiments. The apparatus employed consisted of a warm and a cold water bath, and of pairs of aluminum plates or "thermodes." The latter conducted the heat between the water baths and opposite surfaces of rows of eggs. Thin agar jelly was used as a medium about the eggs to prevent convection and to support the eggs in place. In one series of experiments eggs in the blastula stage were exposed to a horizontal temperature gradient of five degrees (between egg surfaces) for a period of forty hours. The results seem to have confirmed my thesis. While I was not able to demonstrate to my own satisfaction any effect of a transverse gradient on the fundamental bilaterality of the egg, yet there was produced a pronounced asymmetry. The lateral neural folds which developed on the previously warmed side were commonly larger and more active developmentally than the folds on the cooled side (fig. 6A and B). Moreover, the differences were clearly not alone those of developmental "age," but involved the differentiation of a larger amount of material into the neural fold of the warmed side. The thermal gradient definitely affected the physiological expression of the blastula at the time when prospective neural plate material was undergoing determination as a pre-primordium.

I would only suggest by way of explanation of this apparently anomalous relation, that if chorda-mesoderm is the dominant region in relation to which neural plate material is established, then the dorso-ventral gradient is "antagonistic" and the ventro-dorsal gradient "adjuvant," and the results are perhaps those which might be expected.

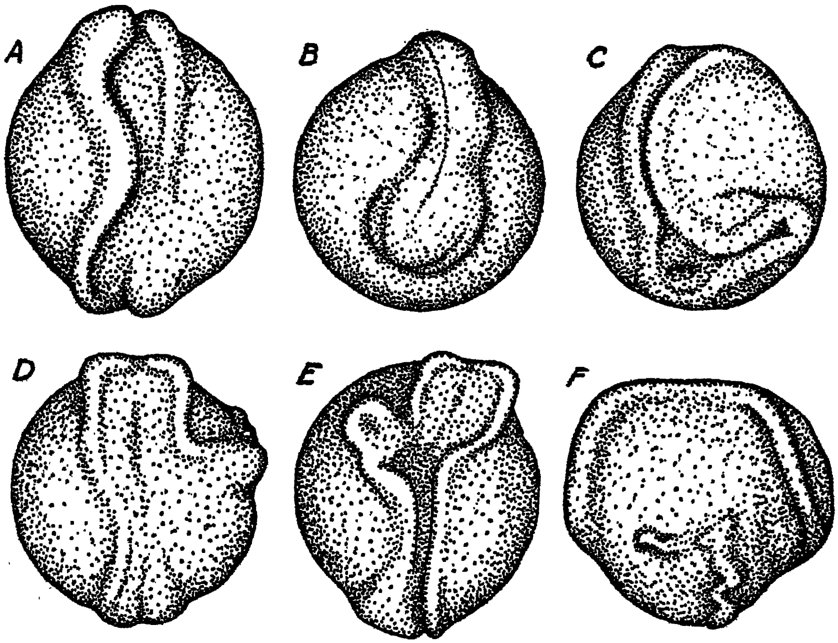

Fig. 6. Effect of Thermal Gradients on Development

Blastulae of *Triturus torosus* were exposed to temperature differentials. *A.* Transverse differentials commonly resulted in a large neural fold on the previously warmed lateral side. *B.* The anterior end of a similar embryo at a later stage in development. Occasionally a secondary neural plate (*C*), an aberrant neural fold (*D*), an accessory brain area (*E*), or puckerings resembling neural folds (*F*) appeared on the previously warmed side. (After Gilchrist, 1928.)

When the gradient was dorso-ventral, the neural plates were sometimes affected in a most unexpected manner. If the dorsal side was warmed they were often smaller, shorter, and with large anterior neural folds. Such results have also been obtained by Dean, Shaw, and Tazelaar (1928); who report also that the converse relationship obtains, there is great proliferation of nervous tissue in specimens cooled dorsally and warmed ventrally.

Reference has been made to the experiments of Vogt (1927, 1928a) in which he subjected eggs to temperature differentials, seeking by cooling to inhibit the development of one half of the egg without at the same time interfering with the normal development of the other half. His aim was "physiological isolation" without morphological isolation. In his 1927 paper he records an effect of his procedure on the rate of development, but no effect on differentiation, a result rather hard to bring into harmony with the work of Huxley and myself. But in his 1928 papers, Vogt not only shows that the thermal differentials do influence differentiation, but he goes beyond Huxley and myself in demonstrating that they produce an actual shifting of the plane of symmetry of the egg toward the warmed side. The eggs of *Pleurodeles* on which he in part worked have a lighter area in what becomes the central portion of the neural plate. He was able to show that the neural fold which forms on the cooled side arises from near the central portion of this area and is hence whiter than its mate. I observed the same color difference in my work with *Triturus*, but failed to perceive its significance, thinking that the unlike pigmentation was an effect of the thermal gradient, as indeed it may in part have been. Vogt, however, has placed his interpretation beyond reasonable doubt by marking the eggs with vital dyes, and then subjecting them to the thermal treatment (fig. 7). His results show clearly that the neural fold of the cooled side is not only smaller than its mate, but that it arises from a more dorsal position.

Vogt interprets the shifting of the neural axis and the inequality in the sizes of the neural folds as secondary and regulative. In view, however, of the discussion which has preceded, I would hold that they reflect actual processes which at the time are in operation. It remains unquestionably true that the temperature differentials did definitely and profoundly modify the process of determination of neural plate material. Taken together, these experiments indicate the presence of a pattern in the egg, possibly quite simple in its nature, which expresses itself functionally in differentiation, and which can be modified by environmental differentials.

Certain other results of my work with eggs of *Triturus* (1928) bear on this subject. In some eighteen instances secondary neural structures appeared on the previously warmed side of the egg. The implication would seem to be that artificial warming produced secondary regions of high physiological activity in relation to which secondary areas of neural plate material differentiated. It is of interest to note that the later fate of the secondary neural material was influenced by its

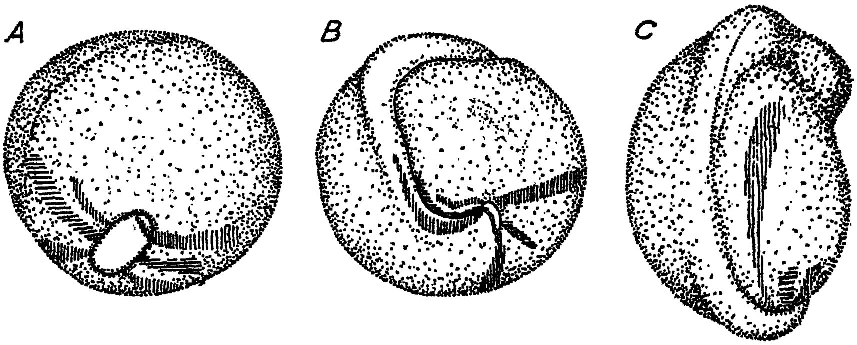

Fig. 7. Effect of a Thermal Differential

An egg of Amblystoma at the four-cell stage was marked symmetrically with vital dye. It was then cooled for three days on the future dorsal-right side. *A.* When removed the egg was in the yolk plug stage; the left neural fold has begun to appear. *B.* Later, the left neural fold has risen up, enclosing the three left marks; but the right fold has not yet appeared. *C.* Still later, the neural folds have closed. The three marks on the right which normally would have been enclosed in the right fold remain as epidermis. (After Vogt, 1928a.)

relation to other regions of the egg. If it were in the neighborhood of the prospective mesoderm of the blastoporal lips, it became underlain by mesoderm and differentiated as a secondary neural plate (fig. 6C). If it were situated anteriorly, but near the primary neural pre-primordium, it became jointed to the latter and produced an aberrant neural fold (fig. 6D) which sometimes differentiated apparently as an accessory brain area (fig. 6E). If, however, it was forward and ventral in position, removed from both the future mesoderm and the future primary neural plate, it differentiated irregularly into structures resembling neural material in cell structure, but quite different in form (fig. 6F).

Putting the various experiments together we conclude that the differentiation is a long process beginning early in cleavage, or even earlier, and continuing actively throughout the blastula stage and even into gastrulation. It takes place in relation to the physiological pattern of the egg, the dominant center of which is at first the animal pole, but later comes to be the dorsal lip of the blastopore. Thermal gradients impressed upon the egg are able to modify the physiological pattern and by so doing affect the position and form of the neural plate.

THE NATURE OF INDUCTION

So much for the nature of the influences in relation to which the early determination of neural plate material takes place. What of the completion of determination through induction arising in underlying chorda-mesoderm? Is the stimulus in this case also of a quantitative and dynamic nature? Huxley (1924), among others, has suggested that such is indeed the case. "It may well be that it is the stimulus of its (the organizer's) activity as such which causes the neighboring cells to differentiate, as would be expected on Child's theory." Mangold (1928b and c) has gone so far as to suggest that the inducing stimulus is of an electric nature, some definite electric potential, although he apparently favors the view that it is of some simple (i.e., not specific) chemical nature. Child (1929) suggests that induction is of the nature of a transmission of energy rather than a transport of particular substances.

There is perhaps evidence that the inducing stimulus is of a quantitative nature in the recent work of Bytinsky-Salz (1929a and b). It will be recalled that Geinitz (1925) found that prospective chorda-mesoderm of anurans when implanted beneath prospective epidermis of *Triton* is able to induce a neural plate and somites. But the reverse does not occur; the chorda-mesoderm of *Triton* will not induce dorsal structures in the anuran. Bytinsky-Salz has taken implants from gastrulae of both urodeles and anurans and inserted them in the archenterons of young *Triton* gastrulae. He finds that prospective epidermis of the anuran gastrulae is not influenced by its urodele host even though it comes to lie in the very substance of the host's chorda-mesoderm. It develops gland cells and ciliated epidermis just as it would have done had it not been transplanted. Are we to conclude that the inducing capacity of *Triton* is not great enough to affect the rapidly developing anuran tissue? In other experiments of Bytinsky-Saltz prospective neural material of a young gastrula (urodele) was placed in the archenteron of another similar gastrula. In its new location it either fuses with the mesoderm of the primary roof, or with the entoderm of the secondary roof, or with the yolk-laden entoderm of the floor of the archenteron. If it joins the mesoderm it forms (by induction) a neural tube or somites.

If it joins the entoderm of the archenteric roof it may develop in the direction of a neural epithelium. If it joins the entoderm of the floor it gives rise to a tissue without definite structural relationships. Are we to conclude that the capacity of materials to induce varies in quantitative fashion, and that the entoderm is of so low an order of activity that it has no inducing influence on material placed within it?

Somewhat more convincing evidence comes from the discovery of Mangold and Spemann (1927) (working independently) that the optic areas of a neural plate taken from an open neural plate stage and inserted into the cleavage cavity of an early gastrula, will induce the formation of a secondary neural plate. There are two stimuli, therefore, prospective chorda-mesoderm of the dorsal lip and the prospective optic area of the open neural plate, either of which if placed in contact with prospective epidermis of a gastrula will induce a neural plate. Mangold (1928a, 1929) has extended his results. He has found that from the middle yolk-plug stage on to embryos showing muscular activity, portions of the brain have this same capacity, although it is best developed during early neural stages. More surprising still is the fact that limb buds taken from young swimming larvae and placed in a similar position will induce what may perhaps be secondary neural structures. Bautzmann (1928b) has found that a young notochord taken from a neurula will exercise the same function; the mesoderm of the somites, however, retains the capacity to a much less degree. Clearly the induction of a neural plate does not depend upon any specific quality of the implant. In each of the above cases, furthermore, the induced secondary neural plates are of the same age as the primary neural plate, no matter what the age of the implant. The *time* of the determination of neural plate material is correlated with the stage in the development of the host; not with the stage in development of the inducing implant.

The *nature* of the structure which is induced depends upon the host and not upon the implant. It depends first upon the *locus* in the host in which the implant is placed. Bautzmann (1929), for example, has shown that the posterior part of the notochord, implanted in an anterior position, induces the formation of anterior parts. Again, it depends upon the *stage* of the host's development. It has been shown that the same optic rudiment which will induce a neural plate in a gastrula, will, if placed beneath the epidermis of a neurula, induce the formation of a lens. The same stimulus (optic rudiment), acting upon the same material (epidermis of host), but at different stages in its development (gastrula, neurula), produces different results (neural plate, lens). The principle has been well expressed with reference to mammalian development by Lillie (1927): "Thus the embryonic ectoderm of a mammal may be said to have the potencies of nervous system, lens, hairs, glands, and epidermis. But these potencies do not exist simultaneously; when the ectoderm has the potency of forming nervous system, it does not have the potency of forming lens or any primordium of later origin." "The specificity," says Lillie, "lies in the stage and locus, not in the inducing agent."

In view of the above considerations we conclude, at any rate for the present, that the property common to different inducing agents is not specific. It is presumably quantitative in its nature. There is no evidence as yet, however, that qualitative and chemical differences do not enter finally into the inductions by which, as

Lehmann shows, contact with chorda and mesoderm determines the form and structure of the neural plate.

SUMMARY

The principal conclusions derived from the experiments just reviewed may be summarized in the following several propositions:

1. The prospective neural plate material of the urodele blastula occupies a crescent-shaped area situated in the upper hemisphere of the egg just above the prospective chorda-mesoderm of the future dorsal blastoporal lip. The convexity of the crescent extends to the animal pole, its concave margin approximates the equator.
2. Prospective neural plate material attains its definitive position as a neural plate during gastrulation, as a result of movements in which its lower concave margin streams toward the descending dorsal lip of the blastopore.
3. From an early blastular stage the prospective neural plate material is "dynamically determined" to perform these characteristic streaming movements of gastrulation. It is thus already a pre-primordium (chemical rudiment).
4. Prospective neural plate material of the blastula is also partially determined materially in that it is independently able to differentiate histologically into neural tissue. This determination is most advanced in the region (neural centrum) which is to be the central portion of the brain area. The bordering zone is less definitely determined. Like other pre-primordia, neural plate material has at first indefinite boundaries.
5. The determination of neural material which occurs before gastrulation is labile in that it is capable of being reversed under the influence of altered surroundings, as transplantation experiments have shown. The neural plate pre-primordium is as yet "relatively indifferent" as to its fate.
6. The determination of neural plate material is completed during gastrulation as a result of an induction originating in the chorda-mesoderm which comes to underlie it: (a) the determination of the neural centrum is rendered irreversible; (b) the mass and extent of the bordering material which goes to form the neural plate is fixed; and (c) the capacity of the material to form a neural tube of normal structure and arrangement is assured.
7. In all, the determination of neural plate material is a continued process of chemical differentiation, which begins early in cleavage or earlier, continues actively throughout the blastular period, and culminates following the movements of gastrulation. The extensive regulatory properties which exist until the process is well nigh completed are to be thought of as primary capacities of the egg, which reflect the mechanism of determination and supply sustained assurance throughout the long process that the final outcome shall be orderly structure.
8. The determination of neural plate material which occurs before gastrulation, presumably takes place in relation to the longitudinal and bilateral structure which the fertilized egg has been shown to possess. Quantitative differences present in the egg (or in its environment) express themselves functionally as physiological gradients and issue qualitatively in diverse types of chemical activity. Presumably the material of high physiological activity surrounding the animal pole is early differentiated (although reversibly) as prospective ectoderm; then that region of prospective ectoderm which is adjacent to the highly active material of the future dorsal lip becomes determined as neural plate substance.
9. Thermal differentials, impressed upon

the egg at the blastular or early gastrular stages, are capable of modifying the physiological pattern, and thus affect the differentiation of neural plate material.

10. The induction which completes the determination of the neural pre-primordium; namely, that which originates following gastrulation in underlying chorda-mesoderm, may also be quantitative, a response to the high rate of physiological activity of the latter substance. More specific chemical influences may enter, however, in determining the precise form and structure of the neural plate.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that The Quarterly Review of Biology *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* The Quarterly Review of Biology, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

OUR FACE FROM FISH TO MAN. *A Portrait Gallery of Our Ancient Ancestors and Kinsfolk togther with a Concise History of Our Best Features.*
By William K. Gregory.
G. P. Putnam's Sons
$4.50 6 x 9; xi + 295 *New York*

This book will find no favor among the fundamentalists. It is too much to expect them even to glance at the frontispiece where in each of the eleven ancestral types of face they can recognize only too easily characteristic features of many of their friends. Rather will it be a source of pleasure to the semi-scientific readers, who, possessed of a keen sense of humor, enjoy mingling in crowds and studying their fellowmen.

Its chief usefulness will be as collateral reading in the college or university course in evolution. This does not mean that it is burdened with all the characteristics of a text book. One can open its pages almost at random and read with interest the story of how we obtained our face, or, merely by studying the 118 excellent illustrations grasp the salient features of our physiognomistical history. The value of the book to the student is increased by its lengthy list of references and its excellent index.

◆

LIFE PROCESSES AND SIZE OF THE BODY AND ORGANS OF THE GRAY NORWAY RAT DURING TEN GENERATIONS IN CAPTIVITY. *Part I. Life Processes, by Helen Dean King. Part II. Size of the Body and Organs, by Henry H. Donaldson. American Anatomical Memoirs, No. 14.*
Wistar Institute of Anatomy and Biology
$3.50 *Philadelphia*
7 x 10½; 106 (paper)

The original plan of the authors was to determine how far towards the ancestral type (the gray Norway) the albino would revert when placed under wild conditions. The mutant albino differs from the wild type not only in lack of pigmentation, but also in the proportional development of its organs. Five colonies of albinos planted in widely different localities having failed to yield results, the reversed experiment is now being tried; namely, of rearing the wild ancestral type in captivity.

As the experiment is to continue over a long period of time and will include a very large number of generations, interim reports are to be issued for time to time. This first preliminary report indicates that results of great significance will be reached as the work progresses. It is based on the data collected on 1539 litters containing 4680 males and 4825 females.

The results show that marked changes have occurred in some of the life processes when the tenth generation of Grays is compared with the first. Growth in early life in the tenth generation is much more rapid than in the first generation. Average body weight of adults (both male and female) shows some increase. As the generations advance, the trend of variability in both sexes of captive Grays is towards that found in stock albinos. Average length of reproductive period has increased by about two months due to earlier breeding. There is marked decrease in sterility and mortality in the later generations, also decided changes in behavior.

A number of changes have occurred in the organ constitution of the captive Grays. The tenth generation shows an increase in body weight on body length and a slight increase in the weight of the hypophysis. There is a decrease in weight of the brain, the thyroid, and the suprarenals (especially in the female), the greater loss in all these organs occurring in the first generation. Comparing the tenth generation of the Grays with the albinos, the brain, the suprarenals (especially in the male), the gonads and the bones are still heavy. Body weight on body length and the weight of the thyroid are similar to those for the albino. The hypophysis, especially that of the female, remains less in weight.

REZENTE WIRBELTIERLEICHEN UND IHRE PALÄOBIOLOGISCHE BEDEUTUNG.

By Johannes Weigelt. *Max Weg*
28 marks *Leipzig*
6½ x 10¼; xvi + 227 + 37 plates
(paper)

This is an extremely important and interesting book, primarily to paleontologists, but also to naturalists generally. It is a study of how animals die in a state of nature, and what then becomes of their bodies. Weigelt's researches on these problems have been systematic and thorough and throw a flood of light on the interpretation of many puzzling phenomena which have been observed in fossil remains. The book is beautifully illustrated with photogravure plates, most of them based on observations made at various points along the Gulf coast and inland in Texas. We strongly recommend the book to anyone interested in evolution.

TEXTBOOK OF EVOLUTION AND GENETICS.

By Arthur W. Lindsey. *The Macmillan Co.*
$3.00 5½ x 8½; xii + 459 *New York*

A well written account of the materials of evolution and genetics and of the theoretical aspects of the subjects. The author aims to hold the balance true between the Darwinian and Lamarckian points of view. The book is a refreshing contrast to most textbooks in its frank recognition of the difficulties still confronting present theories.

THE BOOK OF NATURE. *With the Creator from Season to Season.*

By Marion E. Cady and Frances A. Howell.
Pacific Press Publishing Assoc.
$1.50 *Mountain View, Calif.*
6 x 7½; xvii + 280

A revised edition of a pious treatise designed to start the young on the right path. It can be recommended to all professors of biology in states having anti-evolution laws. They will find it to be just what they need. For example:

> On the sixth morning of creation week cattle and creeping things and beasts of the earth heard the call of God, and they came forth. What fine-looking cattle browsed in the green pastures! Lions, bears, leopards, cats, tigers, dogs, wolves,—animals of all kinds,—roamed the shady woods, and frisked about with the playful lambs. Creeping things, some very tiny, others larger, crawled through the soft grass from bush to bush and from flower to flower.
>
> What a very happy family they were! Animals of all kinds roamed together, ate together, played together, and lay down to sleep side by side. There was no fear or strife among them. Did the bears growl at the little lambs? Did the wolves pursue the sheep? Oh, no! Even the huge elephants stepped about with care, for they would crush the tiny little creatures beneath their feet.
>
> Such were the beasts God created on the sixth day. Why this peace and friendliness among the animals? Ah, sin was not there! Sin brings hatred and strife. When there is no sin, there is friendliness and love. What a comfortable home these creatures found awaiting them! The cattle found their place in the green pastures, the beasts found their place in the shady woods, and creeping things found downy beds in soft grass. Every creature found his place. It was all so wisely planned by a loving Creator.

We had Reginald the Office Boy read this book, he being the youngest member of the staff, and his only comment was that it should have been printed on thinner paper.

GENETICS

L'INDIVIDUALITÈ DU SANG. *En Biologie, en Clinique, et en Médecine Légale.*

By Leone Lattes. *Masson et Cie*
50 francs *Paris*
6¼ x 9⅛; xi + 314 (paper)

An excellent, thorough discussion of individual differences in human blood, especially with reference to iso-agglutinins and blood grouping. The bibliography covers 55 pages of fine print. The book is clearly written, the material well arranged, and the illustrations well reproduced and to the point in their content. Altogether it is one of the best reference sources on the subject covered that we have seen. Successive chapters deal with the individual reactions of normal blood; the heredity of blood individuality; the individuality of the blood as an anthropological datum; clinical applications of blood individuality; the individuality of the blood in forensic medicine; and technique.

* * *

DIE TECHNIK DER BLUTGRUPPENUNTERSUCHUNG FÜR KLINIKER UND GERICHTSÄRZTE. *Nebst Berücksichtigung ihrer Anwendung in der Anthropologie und der Vererbungs- und Konstitutionsforschung.*

By Fritz Schiff. *Julius Springer*
8.60 marks *Berlin*
5⅜ x 8¼; vi + 91 (paper)

The second edition of a useful little handbook of bloodgrouping technique. All bibliography is omitted from the edition and the reader is referred to Lattes (*vide supra*) and Hirszfeld particularly for the literature of the subject.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 290.* Containing following articles: *Methoden der Vererbungsforschung bei Tieren*, by Emil Witschi; *Technik der Variations- und Erblichkeitsanalyse bei Crustaceen*, by Richard Woltereck; *Methoden zur Erforschung der Vererbung bei den Lepidopteren*, by Harry Federley.

Urban und Schwarzenberg
10 marks 7 x 10; 190 (paper) *Berlin*

This number of the Abderhalden *Handbuch* will be found useful by all geneticists, particularly the first article by Witschi. It furnishes an excellent introduction to Mendelian analytical technique.

GENERAL BIOLOGY

UNTERSUCHUNGEN ÜBER DIE ENTSTEHUNG AMÖBENÄHNLICHER ZELLEN AUS ABSTERBENDEN INFUSORIEN. *I. Entstehung, Morphologie und Züchtung der Autoplasmen.*
By Hugo Merton. Walter de Gruyter und Co.
2.20 marks *Berlin*
6¼ x 9⅛; 29 (paper)

This is an extraordinary paper, vouched for (at least to the extent of introducing it to the Heidelberg Academy) by Professor Curt Herbst. The author describes the formation of active, living, and reproducing ameboid organisms from the protoplasm of dying infusoria of three genera, *Vorticella*, *Paramecium*, and *Cyclidium*. He calls these new forms *autoplasm*. The observations are detailed, and seem careful and critical. No mention is made of Bastian, who described what seems to be the same thing many years ago under the name of heterogenesis. But then it has long been fashionable among biologists to regard Bastian as a quack and a faker. Evidence, however, seems to be accumulating which indicates that perhaps he wasn't.

* * *

CONTRIBUTION À L'ÉTUDE DU PEUPLEMENT DES HAUTES MONTAGNES.
By P. Allorge, R. Benoist, A. Chevalier, L. Chopard, L. Germain, H. Heim de Balsac, R. Heim, H. Humbert, R. Jeannel, L. Joleaud, L. Lavauden, R. Maire, E. de Martonne, C. Motas, P. de Peyerimhoff, E. Pittard, J. Sainte-Clair Deville, R. F. Scharf, B. P. Uvarov and A. Vandel. Paul Lechevalier
55 francs 6½ x 10; 259 (paper) *Paris*

A collection of some twenty-one essays on various aspects of the ecology of Alpine habitats. Man, mammals, birds, insects, molluscs, water mites, planarians, and plants are the subjects of papers included in the volume. Unfortunately the volume is not indexed, which diminishes its usefulness for reference.

* * *

THE PUBLIC AQUARIUM. *Its Construction, Equipment, and Management. Department of Commerce, Bureau of Fisheries Document No. 1045.*
By Charles H. Townsend.
U. S. Government Printing Office
25 cents *Washington*
5¾ x 9⅛; 88 (paper)

This report, by the distinguished Director of the New York Aquarium, will be extremely useful to all those who are in any way interested in the problems of successfully managing aquaria. While it deals especially with the construction, equipment and maintenance of the public aquarium, many of the suggestions will be found invaluable in building and operating laboratory aquaria. The numerous illustrations are well chosen. There are two appendices in which are discussed the care of the small aquarium and the treatment for removal of chlorine from city water; while in a third section is given, in tabular form, information regarding thirty-two public aquaria throughout the world.

* * *

VIE ET REPRODUCTION. *Notions Actuelles sur les Problèmes Généraux de la Biologie Animale.*
By Max Aron. *Masson et Cie*
38 francs *Paris*
6⅛ x 9⅛; xi + 366 (paper)

An elementary treatise on general biology, with special emphasis on cytological aspects. The book is intended apparently for popular reading, but will be found interesting by professional biologists and students. It is abundantly and, on the whole, well illustrated.

* * *

A LABORATORY STUDY-GUIDE FOR BIOLOGY.
By Charles A. Gramet.
The School Book Co., Inc.
65 cents 8½ x 10¾; 74 (paper) *New York*

A loose-leaf manual for a high school course in general biology.

* * *

THE PROBLEM OF FERMENTATION. *The Facts and Hypotheses.*
By M. Schoen. Translated from the French by H. Lloyd Hind.
Chapman and Hall, Ltd.
21 shillings net *London*
6 x 9⅝; xii + 211

A remarkably clear presentation of a highly technical subject. The discussions of the hypotheses presented by workers in the various fields of fermentation form by no means the least interesting feature of the book. For the translated edition the author added a new chapter on the rôle of hydrogen in fermentation. A lengthy bibliographical index and subject index add to the usefulness of the book.

HUMAN BIOLOGY

CONSTITUTIONAL INADEQUACIES. *An Introduction to the Study of Abnormal Constitutions.*
By Nicola Pende. Translated by Sante Naccarati. With a Foreword by George Draper.
$3.50 net *Lea and Febiger*
Philadelphia
5¾ x 9¼; 270

It is a real service to all students of human constitution to have this book by the leading Italian investigator in the field made available in English. The book is divided into two parts, of which the first deals with the general concepts of constitutional investigation, or as Pende prefers to call it, *biotypology*. The second part is more special, and deals, on the basis of an organological classification, with localized constitutional anomalies and inadequacies. A final chapter is added as an appendix to the English edition giving briefly a systematic outline of the analysis, from the present day point of view, of the individual biotype. The book is an important contribution to the literature of human biology.

* * *

BORN THAT WAY.
By Johnson O'Connor.
The Williams & Wilkins Co.
$6.00 5¼ x 8; 323 *Baltimore*

One of the volumes of the "Human

Relations Series." The author sums up the results of several years study on selective tests and the value of the applications of such tests in various industries and occupations. Within limits, the results indicate that it is possible to predict the line of work for which the individual is best fitted, or in which he will best succeed. These tests should be of particular value for those who are at the beginning of a career. "In a single morning one may try a complete set of worksamples, the essences of many occupations, vignettes which introduce the chapters of life, and perhaps prove oneself wholly unfit for half, thereby saving many potential failures and years of wasted striving."

Fully half of the book is taken up with appendices giving an interpretation of "worksample grades" and an extension of the Kent-Rosanoff table.

* * *

PRIMITIVE ART.

By Franz Boas.

H. Aschehoug and Co. (W. Nygaard)
$7.75 7 x 9; 376 *Oslo*

In this book Professor Boas gives an analytical description of the fundamental traits of primitive art, illustrated by many examples not only of carving, basketry, weaving, pottery and metal work, but of literature, music and the dance. In all these arts rhythm is an important element. He concludes that geometrical patterns do not grow out of realistic representation.

It is interesting to note that Boas does not agree with Lévy-Bruhl as to the "prelogical" character of primitive thought.

> There must have been a time when man's mental equipment was different from what it is now, when it was evolving from a condition similar to that found among the higher apes. That period lies far behind us and no trace of a lower mental organization is found in any of the extant races of man. So far as my personal experience goes and so far as I feel competent to judge ethnographical data on the basis of this experience, the mental processes of man are the same everywhere, regardless of race and culture, and regardless of the apparent absurdity of beliefs and customs.
>
> Some theorists assume a mental equipment of primitive man distinct from that of civilized man. I have never seen a person in primitive life to whom this theory would apply. There are slavish believers in the teachings of the past and there are scoffers and unbelievers; there are clear thinkers and muddleheaded bunglers; there are strong characters and weaklings.
>
> The behavior of everybody, no matter to what culture he may belong, is determined by the traditional material he handles, and man, the world over, handles the material transmitted to him according to the same methods.
>
> Our traditional experience has taught us to consider the course of objective events as the result of definite, objective causation. Inexorable causality governs here and the outer world cannot be influenced by mental conditions. Hence our hesitating wonder at the phenomena of hypnotism and suggestion in which these lines seem no longer sharply drawn. Our cultural environment has impressed this view upon our minds so deeply that we assume as a fundamental fact that material phenomena, particularly outside of the field of human behavior, can never be influenced by mental, subjective processes. Still, every ardent wish implies the possibility of fulfilment and prayers for objective benefits or for help do not differ in principle from the attempts of primitive man to interfere with the uncontrollable course of nature. The credulity with which fantastic theories bearing upon health are accepted, the constant rise of religious sects with abstruse dogmatic tenets, as well as the fashions in scientific and philosophic theory prove the weakness of our claim to a rational view of the world.
>
> Anyone who has lived with primitive tribes, who has shared their joys and sorrows, their privations and their luxuries, who sees in them not solely subjects of study to be examined like a cell under the microscope, but feeling and thinking human beings, will agree that there is no such thing as a "primitive mind," a "magical" or "prelogical" way of thinking, but that each individual in "primitive" society is a man, a woman, a child of the same kind, of the same way of thinking, feeling and acting as man, woman or child in our own society.

DISCOVERIES AND ADVENTURES IN CENTRAL AMERICA.

By Thomas Gann. Charles Scribner's Sons
$5.00 5¾ x 9; 261 *New York*

Mr. Gann continues to discover ruined Maya cities in the jungle and to write in his usual fascinating way about his finds and the wild life which he encounters. We can recommend the book to all those interested in the Maya civilization or in exciting stories of adventure.

THE LAND PIRATES OF INDIA.

By W. J. Hatch. J. B. Lippincott Co.
$5.00 5½ x 8½; 272 *Philadelphia*

An interesting account of the life and habits of the Kuraver, a section of one of the great robber castes of South India. They are trained from babyhood in the arts of deceit and thievery, and become extremely expert at both. In the main they have no fixed abode but live a wandering gypsy life. The book is of real interest to the thoughtful student of human biology, as well as entertaining to the general reader.

THE SAVAGE SOLOMONS AS THEY WERE AND ARE: *A Record of a Head-hunting People Gradually Emerging from a Life of Savage Cruelty and Bloody Customs, with a Description of their Manners and Ways and of the Beauties and Potentialities of the Islands.*

By S. G. C. Knibbs.
Seeley, Service and Co., Ltd.
21 shillings 5¼ x 8½; 282 *London*

A pleasantly discursive account of the author's experiences while acting as a government land surveyor, and later Commissioner of Lands in the British Solomon Islands Protectorate. His observations on anthropological and ethnological matters are too casual to be of much value, but the book makes interesting reading.

URENTWICKLUNG DES MENSCHEN.

Tatsachen und Gedanken.

By Artur Neuberg. C. Bertelsmann
13 marks *Gütersloh*
6½ x 9½; viii + 426

The author of this treatise is an *evangelische Theolog*, of the Lutheran persuasion. It is a *résumé* of all science, but especially biology and geology, from the point of view of an intelligent, widely read parson. As a "reconciler," and that is what it is all about, Pastor Neuberg makes the current American practitioners in this domain seem shoddy. His bibliography and notes run to over 25 pages of fine print. For those who like this sort of thing it is quite the best book of its kind we have seen. It is a pious scientific tract, which does not nauseate.

THE BEAUMONT FOUNDATION LECTURES. *Series Number Seven. I. Human Constitution. Its Significance in Medicine and How it May be Studied. II. The Influence of Sex in Determining Human Disease Potentiality. III. The Patient and His Physician.*

By George Draper.
The Williams & Wilkins Co.
$1.00 5⅛ x 8; ix + 75 *Baltimore*

The three papers which make up this little volume constitute the seventh series of Beaumont Foundation Lectures before the Wayne County Medical Society. The first two essays will serve as a useful and entertaining introduction to the general biological reader who wants to know something of the present viewpoint regarding the study of constitution in relation to disease. Unfortunately the preparation of the material for printing has been very carelessly done. Errors in spelling authors' names and similar slips mar an otherwise commendable volume.

PHYSICAL EDUCATION IN CITY PUBLIC SCHOOLS. *Physical Education Series No. 10.*

By Marie M. Ready.
U. S. Government Printing Office
15 cents *Washington, D. C.*
$5\frac{7}{8}$ x $9\frac{1}{8}$; iv + 100 (paper)

As the result of a questionnaire sent to the superintendants of schools and directors of physical education of a large number of cities, we find in this bulletin much detailed information about physical education practices in American public schools. How far these data will serve the inquirer desirous of assessing the effectiveness of our physical education program is another question. From the table on special costumes required in the gymnasium we learn that in Hannibal, Mo. and other cities "only shoes are required." To a ribald mind the interpretation of this might seem ambiguous.

AN ANALYSIS OF LIFE. *An Attempt to Conduct an Independent Enquiry into the Leading Problems which Confront Mankind.*

By Harold Clunn. Simpkin, Marshall, Ltd.
5 shillings net *London*
$5\frac{3}{8}$ x $8\frac{1}{2}$; xxiv + 247

This is a quasi-religious and ethical tract rather than a biological one. Its philosophical position is bred out of Pollyanna by a Monist. The author forecasts

> a glorious future for the human race, when the present day standards of morality and intellect, great as these may now appear to a considerable number of people, will be superseded by the higher standards of conduct which have been built up and improved upon by countless succeeding generations, each of which has profited by the increased experience of its predecessor. When that stage in the history of mankind has been reached, the present-day standards of morality and conduct may even appear almost as primitive as those of the Stone Age seem to the most advanced peoples of our own time.

UNDISCOVERED AUSTRALIA. *Being an Account of an Expedition to Tropical Australia to Collect Specimens of the Rarer Native Fauna for the British Museum, 1923–1925.*

By Sir G. H. Wilkins. G. P. Putnam's Sons
$4.50 6 x $8\frac{3}{4}$; xiii + 353 *New York*

An unimportant but fairly interesting account of the well-known author's travels in Australia while collecting material for the British Museum (Natural History). Speaking of the natives assembled at the Mission Station on Milingimbi, one of the Crocodile Islands, Wilkins makes the following observation (p. 157):

> A curious physiological feature was noticed in many of these unclothed people. They exhibited two or three joints of the lower vertebrae in the form of a tail. The tail was not so noticeable on these people as it is on some of the African tribes, but the tails were quite conspicuous enough to show in a photograph.

Facing page 145 is a photograph of a woman showing one of these "tails." More and more convincing evidence about them would have been welcome. Reginald our Office Boy, who has fundamentalist leanings, but is otherwise sceptical, says that the thing photographed looks to him more like a misplaced wen than a tail.

TRAVELS AND SETTLEMENTS OF EARLY MAN. *A Study of the Origins of Human Progress.*

By T. S. Foster. Frederick A. Stokes Co.
$7.50 6 x $9\frac{5}{8}$; 320 *New York*

This is perhaps the best synthesis that has yet been written about our present knowledge of prehistoric man. Certainly we have seen no other attempt at a reconstruction of his life and thought which is based upon so sound and penetrating a philosophic background. The first chapter, which is an essay on history and education in general, is superb. The author's knowledge in the fields of anthropology, archaeology and history is wide and deep. We have noted no errors except trivial and obvious slips of the pen. The work is scholarly without being pedantic. Unfortunately it is not easy reading. The style is heavy and at times involved, and on this account we judge that the publisher's hope for a general audience, which is yearningly expressed in the jacket blurb, will prove a vain one. But to the serious student of human biology we strongly recommend this volume.

CHILDREN IN AGRICULTURE. *U. S. Department of Labor, Children's Bureau Publication No. 187.*

By Nettie P. McGill.
U. S. Government Printing Office
25 cents *Washington*
$5\frac{3}{4}$ x 9; v + 81 (paper)

A summary of the main results of investigations of the work of children in agriculture, obtained from published reports by the Children's Bureau and other sources. Included in the report is a discussion of child labor laws in the various states, a bibliography, and tables (44 in number) exhibiting the number, age, and sex of children engaged in farm work, as well as the type of work performed, prepared from the census data of 1920. It is interesting to note that while there is little legislation anywhere which specifically interferes with the labor of children on farms, except what indirectly comes from compulsory school attendance laws, the only states which in 1920 had more than 10 per cent of the children aged 10 to 15 engaged in agricultural pursuits were Alabama, Arkansas, Georgia, Mississippi, North Carolina, South Carolina, Tennessee, and Texas. As examples of northern farming states for comparison, Illinois had only 0.8 per cent, and Iowa 1.5 per cent.

STUDIES IN PHYSICAL DEVELOPMENT AND POSTURE. *I. The Effect of Exercise on the Physical Condition and Development of Adolescent Boys. II. Bodily Growth with Age. III. Physical Fitness as Reflected in Tests of Muscular Strength. Public Health Bulletin No. 179.*

By Louis Schwartz, Rollo H. Britten and Lewis R. Thompson.
U. S. Government Printing Office
30 cents *Washington*
$5\frac{3}{4}$ x 9; xii + 124 (paper)

These studies are grouped under three headings: The effect of exercise on the physical condition and development of adolescent boys; bodily growth with age; physical fitness as reflected in tests of muscular strength. They comprise part of a plan for an investigation of the effects of occupation in the causation of faulty posture. As no actual data existed which could be used as a basis for the more specialized study, it was necessary to determine statistically the types of posture which might be considered normal for the average individual when occupation was not an important factor. In addition to numerous measurements of the body there were tests for ascertaining vital capacity, lung force and lung fatigue, and records made of systolic and diastolic blood pressures, and of the pulse at rest, immediately after exercise and two minutes after exercise. Three photographs were taken of each individual. Altogether 2200 individuals living in New York City were examined, all being white males whose parents were born in the United States. Included in the text are 69 tables and 62 figures. This monograph will be a valuable source reference for students of constitution in particular. The results are too detailed and manifold to permit of brief review.

* * *

REFRACTIVE ERRORS IN THE EYES OF CHILDREN AS DETERMINED BY RETINOSCOPIC EXAMINATION WITH A CYCLOPLEGIC. *Results of Eye Examinations of 1,860 White School Children in Washington, D. C. Public Health Bulletin No. 182.*
By Grover A. Kempf, Selwyn D. Collins and Bernard L. Jarman.
U. S. Government Printing Office
15 cents *Washington*
5¾ x 9; v + 56 (paper)

An extensive study on the eyes of 1860 white school children of varying ages in Washington, D. C. The work was undertaken to determine "among other things, the real prevalence of refractive errors of various types and degrees at different ages, and whether there is any age period during which myopia or other refractive errors are particularly likely to develop." Homatropin was used as a cycloplegic. The results, too detailed to be given in a brief summary, add valuable data to the literature of anthropometry. In the text are 14 figures and 17 tables, while in the appendix are given further tables of distribution and correlation.

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ANTHROPOMETRIE. *Anleitung zu Selbständigen Anthropologischen Erhebungen.*
By Rudolf Martin. *Julius Springer*
4.80 marks *Berlin*
6¾ x 10⅛; 51 (paper)

This new edition of this well known little handbook of anthropometric technique is practically unchanged from the original edition, beyond the correction of minor errors in proof-reading, etc. Some new illustrations and formulae have been added. It is a standard work in its field.

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HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 289.* Containing following articles: *Die Statistik als Hilfsmittel der klinischen Nosographie,* by Otto Körner; *Methoden zur Bestimmung der Wurzelfestigkeit und des Neigungswinkels menschlicher Haare,* by Adolf Basler; *Über die Methodik der Zellstimulation,* by Methodi Popoff; *Methodik der funktionellen Extremitätentransplantation,* by Paul Weiss; *Bestimmung der Lage der optischen Achse in Biokristallen,* by W. J. Schmidt.
Urban und Schwarzenberg
8 marks 7 x 10; 116 (paper) *Berlin*
Lieferung 292. Die Methoden der konstitutionellen Körperbauforschung.
By Friedrich v. Rohden.
Urban und Schwarzenberg
10 marks 7 x 10; 173 (paper) *Berlin*

The first of the articles in *Lieferung* 289 is an excellent account of the pitfalls which must be avoided in statistical investigations on clinical data. The other articles in this number are perhaps of less importance, and chiefly of general biological interest. The account of the technique of constitutional studies by von Rohden is excellent, and will be valued by all workers in that field.

CHILDREN OF ILLEGITIMATE BIRTH WHOSE MOTHERS HAVE KEPT THEIR CUSTODY.

U. S. Department of Labor, Children's Bureau Publication No. 190.
By A. Madorah Donahue.
U. S. Government Printing Office
20 cents *Washington*
5¾ x 9⅛; v + 105 (paper)

A study for determining the desirability of keeping such children in the custody of their mothers. The cases reported are of 253 children, from 8 years to manhood and womanhood, representing 241 mothers. Twenty-seven organizations in 11 cities made reports on schedule forms, prepared by the Children's Bureau. Additional data were obtained in many cases on various phases of the general subject: the personal history and character of the child's father and mother; the effect on the child of the knowledge of his illegitimate birth if he was aware of it, etc.

Social workers have found that mothers who care for their illegitimate children during early infancy will, in most cases, assume responsibility for them permanently, either directly or with the assistance of near relatives. The present study shows that with but few exceptions such children are successfully absorbed into the life of their communities. The best place to bring up an illegitimate child, in short, is in its own family. Thus again has the Children's Bureau achieved a blinding glimpse of the obvious. There is an appendix outlining the method of the investigation.

WANDERINGS IN WILD AUSTRALIA.

In two volumes.
By Sir Baldwin Spencer. The Macmillan Co.
$17 per set *New York*
5¾ x 8⅝; xlii + 930

These extraordinarily interesting volumes are packed with information of interest to the anthropologist and the zoologist. The work is composed of the distinguished author's diaries kept during his various expeditions in the Australian bush, edited and expanded. Originally a zoologist, and never losing his interest in that subject, Baldwin Spencer came to be recognized as one of the leading anthropologists and ethnologists of the world.

Because of the wealth of detail recorded in these stately volumes it is impossible to make any brief abstract of the contents. One can only choose special points for mention, which happen to lie in the field of one's own particular interest. For example: We are told that the native recognizes no such thing as natural death. If a person dies he has been killed by someone, either directly or through the intervention of magic. How strong the native's belief on this point is, and also the extraordinary effect which the mind may have on the body, are illustrated by the following quotation (I, pp. 256–257):

> Any native who believes that he has been struck by a charmed spear is almost sure to die, whether the wound be slight or severe, unless he be saved by the counter-magic of a medicine man. There is no doubt whatever that a native will die after the infliction of even a most superficial wound if only he believes the weapon which inflicted the wound had been 'sung' over and thus endowed with *Arungquilta*. He simply lies down, refuses food and pines away. Not long ago a man from Barrow Creek received a slight wound in the groin. Though there was apparently nothing serious the matter with him, still he persisted in saying that the spear had been charmed and that he must die, which accordingly he did in the course of a few days. Another man coming down to

> Alice Springs from Tennant Creek contracted a slight cold, but the local men told him that members of a group of about twelve miles away to the east had taken his heart out, and believing this to be so, he simply laid himself down and wasted away. In a similar way a man at Charlotte Waters came to us with a slight wound in his back. He was assured that the wound was not serious, and it was dressed in the usual way, but he persisted in saying that the spear had been 'sung,' and that it could not be seen, yet in reality it had broken his back and he was going to die, which accordingly he did. As the result a party was organised among the members of his group to avenge his death, and the man who was supposed to have wounded him with the charmed weapon was killed.
>
> Instances of occurrences such as these could be multiplied, and though, of course, it is impossible to prove that death would not have followed under any circumstances—that is, whether the native had or had not imagined the weapon to have been 'sung'—yet, with a knowledge of what wounds and injuries he will survive if he does not suspect the intervention of magic, it is not possible to explain death under such circumstances except as associated with the firm belief of the injured man that *Arungquilta* has entered his body, and that therefore he must die.

The volumes are beautifully and lavishly illustrated. They are as fascinating reading as a novel.

SOME PROBLEMS OF LONGEVITY.

By Frederick L. Hoffman. The Spectator Co.
$6.00 5 x 8; x + 180 *New York*

Dr. Hoffman is a vigorous and always interesting writer on public health topics. In the 35 brief chapters in this book he discusses as many different phases of the problem of longevity and related topics, frequently drawing upon his wide knowledge of vital statistics to illustrate his points. Among some of the matters discussed we find: The marital death rate; wasted children's lives; the health of primitive man; the health of the negro; what causes death; social diseases; small pox and vaccination; the human constitution; living underground; tired of life; etc. Unfortunately the book lacks an index.

COMMUNITY HYGIENE.

By Dean F. Smiley and Adrian G. Gould.
The Macmillan Co.
$2.00 5 x 7$\frac{3}{4}$; x + 350 *New York*

In this companion volume to their *College Textbook of Hygiene*, reviewed in our issue of December, 1928, the authors "present those facts concerning the promotion and safe-guarding of public health which they feel should be an essential part of the mental equipment of every college man or woman." The book is interestingly, and on the whole sanely, written, though perhaps a little soft-boiled towards the claims of results from some of the public-health activities.

POSTERITY *in the Light of Science, Philanthropy, and Population.*

By Frank W. White. Watts and Co.
2 s. 6 d. net *London*
4$\frac{3}{4}$ x 7$\frac{1}{8}$; ix + 139

Mr. White is evidently one of the fortunate tribe from whom no secrets are hid. In the 139 pages of his book are given neat eugenic solutions of virtually all the problems with which the British Empire is confronted. We doubt, however, whether the reformer who tried to put the suggested program into practice would find it either as easy or as efficacious as Mr. White himself seems to believe. Major Leonard Darwin, in his Foreword, says that the author is more hopeful than he is.

EXTENSION METHODS AND THEIR RELATIVE EFFECTIVENESS. *U. S. Department of Agriculture Technical Bulletin No. 106.*

By M. C. Wilson.

U. S. Government Printing Office
15 cents *Washington*
5¾ x 9⅛; 47 (paper)

A study of how far the $20,000,000 which is expended annually in the United States for extension work in agriculture and home economics is effective in persuading farmers and their families to adopt the improved practices. In the areas studied the proportion of amenable families ranged from 59 to 96 per cent for agricultural practices and from 10 to 65 per cent for home-economics practices. News stories are the most effective extension method in proportion to their cost.

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A STUDY OF ENDEMIC PELLAGRA IN SOME COTTON-MILL VILLAGES OF SOUTH CAROLINA. *Hygienic Laboratory Bulletin No. 153.*

By Joseph Goldberger, G. A. Wheeler, Edgar Sydenstricker and Wilford I. King, with the cooperation of Wm. S. Bean, Jr., R. E. Dyer, J. D. Reichard, P. M. Stewart, M. C. Edmonds, R. E. Tarbett, Dorothy Wiehl, and Jennie C. Goddard.

U. S. Government Printing Office
20 cents. *Washington, D. C.*
5⅞ x 9⅛; vi + 85 (paper)

A careful study of the relation of various demographic, sanitary, economic and dietary factors to pellagra incidence. Among the authors' findings are the following: that endemic pellagra is most frequent in children of from two to fifteen years of age; that the fatality rate is probably not over 3 per cent; that single women, as compared with married, widowed or divorced, are relatively exempt; that 80 to 90 per cent of all cases had their onset from April to July, inclusive; that any association of pellagra with sanitary conditions is a result of the association of both with economic status; that there is a high negative correlation of pellagra with family income; that year-to-year changes in the incidence of the disease parallel changes in economic conditions. The suggested explanation is that these results are caused by differences in the pellagra-preventive value of the diet.

* * *

STATISTICAL ABSTRACT FOR THE UNITED KINGDOM *for each of the fifteen years from 1913 to 1927. Seventy-second number.*

Board of Trade (In conjunction with the Ministry of Labour and the Registrar-General).

His Majesty's Stationery Office
6 s. 6 d. 6 x 9⅝; xv + 377 (paper) *London*

The usual well arranged summary containing not only annual figures from 1913 to 1927 but also in many cases decennial figures extending back to 1851 or earlier. We note that while the number of premises licensed to sell intoxicating liquors decreased from 112,371 in 1913 to 101,504 in 1927, a reduction of 9.7 per cent, the number of convictions for drunkenness decreased from 188,877 in 1913 to 65,166 in 1927, a reduction of 65.5 per cent. Apparently prohibition is not the only way of dealing with the alcohol problem.

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THE MAKING OF A GREAT RACE. *Racial and Religious Cross-Currents in the United States.*

By Edward A. Steiner. Fleming H. Revell Co.
$1.75 5 x 7⅜; 192 *New York*

In this book, the author, for many years a student of the immigrant and his problems, presents his views on the cultural value of the three dominant religious groups in the United States—Jews, Roman Catholics, and Protestants—in the making of the future American race. Mr. Steiner is an optimist. His final conclusion is:

> Something, somewhere, assures the bravely humble that here on this continent we may develop a great culture in which the soul of man will be of supreme value; in which personality, not property, will be the measure of achievement, and that a time will come when we will graft all the religious cultures and racial inheritances into unity, making an American culture of universal worth and eternal value.

The book lacks an index.

SPINOZA.

By Leon Roth. Little, Brown, and Co.
$3.00 5½ x 8½; xvi + 250 *Boston*

This admirable monograph, by the first professor of philosophy at the Hebrew University of Jerusalem, forms one of the opening volumes of the new "Leaders of Philosophy" Series. It has been written for the general reader as well as the student. The first few chapters are devoted to the life and character of Spinoza, his works and general outlook. The author then enters upon a discussion of the philosophy of the great Dutch scholar, the sources from which he derived his thought and an estimate of his influence upon his contemporaries. Perhaps one of the most valuable contributions which the book makes to the history of philosophy is in the section devoted to the trend of philosophic thought in Spinoza's time. Professor Roth quotes at length from the correspondence between Spinoza and some of his opponents, chiefly Blyenbergh and Tschirnhaus. In these discussions are foreshadowed the reactions of later philosophers to the Spinozian concepts.

THE AMERICAN NEGRO. *The Annals of the American Academy of Political and Social Science, Vol. CXXXX, No. 229.*

American Academy of Political and Social Science
$2.00 (paper) *West Philadelphia*
$2.50 (cloth)
6½ x 9½; viii + 359

A collection of some thirty-nine papers dealing with various aspects of Negro civilization in America at the present time. The material is grouped under seven general heads, as follows: Race relations; the Negro as an element in the population of the United States; the legal status of the Negro; the economic achievement of the Negro; organization for social betterment; race relations in other lands. The volume is edited by Prof. Donald Young. It is an important contribution to human biology.

SOCIETY AND ITS PROBLEMS. *An Introduction to the Principles of Sociology.*

By Grove S. Dow. Thomas Y. Crowell Co.
$3.00 5¼ x 7⅞; xiii + 707 *New York*

A revised third edition and fifteenth printing of a book which is widely used as a text-book, as well as by workers in social and philanthropic fields. The edition has been entirely reset and expanded, statistical and other data have been brought up to date and two entirely new chapters on Cultural Forces and Social Processes added. Perhaps the outstanding feature in this edition, when compared with previous ones, is the addition and expansion of much theoretical material, not only in those portions devoted to pure theory, but in other sections of the book as well.

ZOOLOGY

PAPERS FROM THE TORTUGAS LABORATORY OF CARNEGIE INSTITUTION OF WASHINGTON. *Volume XXVI. Publication No. 391.*
Carnegie Institution of Washington
$2.50 (paper) 6¾ x 10; 257 *Washington*
$3.50 (cloth)

Among the most interesting of these papers are that of Tennant, Taylor and Whitaker, who find that both halves of a sea-urchin egg, no matter what the plane of section, may form normal identical larvae; Gudger's paper on the teleost fishes of the Tortugas, in which he concludes that it is dangerous to base the classification of tropical fishes on coloration or on the description of a single specimen; Pearse's paper on migration from marine to terrestrial habitats; and Lipman's studies on marine bacteria, which do not bear out the Drew hypothesis of $CaCO_3$ precipitation in the sea through the agency of bacteria.

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THE BUREAU OF BIOLOGICAL SURVEY. *Its History, Activities and Organization. Institute for Government Research. Service Monographs of the United States Government No. 54.*
By Jenks Cameron. The Johns Hopkins Press
$2.00 5½ x 8⅝; x + 339 *Baltimore*

This is one of the series of monographs in which the Institute for Government Research is dealing with each of the fifty or more distinct services of the government. It describes the background and history of the Biological Survey, its activities of wild life investigation, encouragement, discouragement and protection, and its organization, with the following appendices: Outline of organization; Classification of activities; Publications; Laws; Financial statements; Miscellaneous statistics; and Bibliography. The monograph is well written and will be a valuable source of information.

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THE TERRESTRIAL SHELL-BEARING MOLLUSCA OF ALABAMA. *University of Michigan, Museum of Zoology, Miscellaneous Publication No. 18.*
By Bryant Walker. Published in Co-operation with the Geological Survey of Alabama and the Alabama Museum of Natural History.
University of Michigan
$1.00 *Ann Arbor*
6¾ x 10; 180 (paper)

A useful handbook, well illustrated, for the identification of land snails. Workers in other states than Alabama will find it valuable.

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THE HERPETOLOGY OF MICHIGAN. *Michigan Handbook Series, No. 3.*
By Alexander G. Ruthven, Crystal Thompson and Helen T. Gaige. Uinversity of Michigan
$1.50 *Ann Arbor*
5⅛ x 7½; ix + 229 (paper)

THE WHIP SNAKES AND RACERS. *Genera Masticophis and Coluber.*
By Arthur I. Ortenburger.
University of Michigan, General Library
$6.00 *Ann Arbor*
8 x 10½; xviii + 247

Under the distinguished leadership of its Director, Dr. Alexander G. Ruthven, the University of Michigan has become famous as a center of herpetological research. These two volumes are substantial contributions to the enhancement of this high reputation. The first is a well illustrated handbook for the identification of the amphibia, snakes, and turtles of Michigan. Data on distribution within the state are given in sufficient detail, in many cases by spot maps. This book will be invaluable to teachers of natural history, nature study, etc.

The second volume noted is a thorough, solid piece of taxonomic research, monographic in character. It is beautifully illustrated by photographic plates as well as line drawings.

CENTENARY HISTORY OF THE ZOOLOGICAL SOCIETY OF LONDON.

By P. Chalmers Mitchell.

Zoological Society of London
25 shillings *London*
5½ x 8½; xi + 307

Sir Peter Chalmers Mitchell has added not a little to the considerable indebtedness which all zoologists already owe him by preparing this history of the first hundred years of the existence of the Zoological Society of London. It is entertainingly written, and at the same time a valuable contribution to the records of the history of science. The Zoological Society may well be proud of its record of achievement. Its publications have uniformly maintained a very high standard of excellence; its Zoological Garden in Regent's Park has long been the world model for such institutions; and in keeping up the publication of the *Zoological Record* a service of inestimable value to the progress of systematic zoology has been performed. With an annual income running at present above $700,000 a year and likely to increase, the future looks bright. We feel certain that all American zoologists will join with us in congratulating the Society and its efficient Secretary on its achievements and its prospects.

FAUNE ENTOMOLOGIQUE DE LA PROVINCE DE QUÉBEC. *Vol. IV. Sixième Ordre. Les Lépidoptères. Fascicule I. Diurnes.*

By l'Abbé L. Provancher and le Chanoine V.-A. Huard. *Franciscaine Missionnaire*
$1.00 *Quebec*
6¼ x 9¼; xi + 101 (paper)

This fascicle, published in 1929, is the continuation of an enterprise begun in 1877. It gives directions for collecting and mounting butterflies, followed by systematic descriptions of the diurnal species which have been recorded in Quebec. The rather infrequent illustrations are not very successful, being mostly muddy and blurred half-tones in the text.

DIE NEDERLANDSCHE BEEK-TRICLADEN EN DE OORZAKEN VAN HAAR VERSPREIDING.

By A. D. Voûte.

Zuid-Hollandsche Boek- en Handelsdrukkerij
6 shillings *'s-Gravenhage*
6¼ x 9¼; 116 (paper)

A doctoral dissertation on the local distribution of planarians in Holland, considered from the ecological and behavioristic viewpoints. The author concludes that neither *Planaria alpina* nor *Polucelis cornuta* can be regarded as glacial-period relicts in their Dutch habitats.

PRINCIPLES OF FOREST ENTOMOLOGY.

By Samuel A. Graham.

McGraw-Hill Book Co., Inc.
$3.50 5¾ x 9; xiv + 339 *New York*

As its name implies this is not a handbook of all the species of insects that feed on trees, but a well written discussion of the relations between forest insects and their environment and of the bearing of these principles on problems of insect control in forestry. In his treatment the author uses Chapman's concepts of biotic potential—the ability of a species to multiply in a given time when placed under the most favorable conditions—and environmental resistance—the sum of all the factors in an environment that tend to reduce the rate of insect multiplication. As the biotic potential is constant for a given species it follows that if any factor in the environmental resistance decreases without a compensating increase in other factors, the biotic balance is upset and the species may become epidemic. Control operations are then necessary to restore the environmental resistance to its former level. The book discusses in detail the various methods of control and the various ecological groups of forest insects with examples taken from the more important pests.

SCIENCE OF THE SEA. *An Elementary Handbook of Practical Oceanography for Travellers, Sailors, and Yachtsmen.*

Prepared by the Challenger Society for the Promotion of the Study of Oceanography. Originally edited by G. Herbert Fowler. Second Edition edited by E. J. Allen.
Oxford University Press
$6.00 5¾ x 8⅞; xxiii + 502 *New York*

"Not seldom those who are engaged in oceanographic work are asked by some one about to start on a long voyage: 'How can I do some work for science? I don't know anything about it; where can I "read it up"?'" This book, designed to give the needful information to such amateurs, has set at least one reader wild to go on an oceanographic expedition of his own. We note that Professor D'Arcy Thompson thinks there is something in the sea-serpent.

THE COWBIRDS. *A Study in the Biology of Social Parasitism.*

By Herbert Friedmann. *Charles C. Thomas*
$6.00 net *Springfield, Ill.*
6½ x 9½; xvii + 421

This is a contribution of first rate importance to natural history, ecology, animal behavior and evolution. The book is extensively and well illustrated by original photographs. It is beautifully printed and does great credit to the publisher as well as the author.

Five years of study in central New York, in Argentina, and on the Texan-Mexican border have yielded Dr. Friedmann a rich harvest of knowledge of the natural history of the Cowbirds and especially of nest parasitism, a habit which they share with the cuckoos and a few other forms. His conclusion is that "the immediate cause of the origin of the parasitic habit in the Cowbirds was the loss of the protecting instinct of the male." There is a bibliography of 36 pages.

COMPARATIVE ZOOLOGY. *An Introduction to the Study of Comparative Anatomy, Comparative Embryology and Taxonomy.*

By Cecil von Bonde. *Juta and Co., Ltd.*
21 shillings *Capetown*
5¼ x 8¾; v + 240

A text book in which the divisions are I. Comparative Anatomy; II. Comparative Embryology; III. Taxonomy.

ANIMAL PARASITOLOGY. *With Special Reference to Man and Domesticated Animals.*
By Robert Hegner, Francis M. Root and Donald L. Augustine. *The Century Co.*
$6.50 5$\frac{3}{4}$ x 8$\frac{3}{4}$; xxi + 731 *New York*

This encyclopedic textbook consists of an introduction on Parasitism in Animals and a section on Protozoology by Hegner, and sections on Helminthology by Augustine and on Medical Entomology by Root. The parasites of man are emphasized, and those of domestic animals are described whenever possible. There is a bibliography of 57 pages and author and subject indexes.

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A TEXTBOOK IN GENERAL ZOOLOGY.
By Henry R. Linville, Henry A. Kelly and Harley J. Van Cleave. *Ginn and Co.*
$1.80 5$\frac{1}{8}$ x 7$\frac{1}{8}$; viii + 463 *Boston*

A revision by Van Cleave of Linville and Kelley's *Textbook in General Zoology.* It is designed as the basis for a full year's course for students beginning the subject. In the revision an attempt has been made to give a distinct biological orientation of the subject. The book is interestingly written and well illustrated.

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BOTANY

LEAF TEMPERATURES OF COTTON AND THEIR RELATION TO TRANSPIRATION, VARIETAL DIFFERENCES, AND YIELDS. *United States Department of Agriculture Technical Bulletin No. 91.*
By Frank M. Eaton and Galen O. Belden.
U. S. Government Printing Office
10 cents *Washington*
5$\frac{3}{4}$ x 9$\frac{1}{8}$; 40 (paper)

Thermo-electric measurements show differences among cotton varieties in departure of the leaf temperature from the temperature of the air. The variety with high leaf temperatures has shown poor yields in years with high summer temperatures, whereas the variety with lower leaf temperatures has shown no such relation.

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THE GENUS HAPLOPAPPUS. *A Phylogenetic Study in the Compositæ. Carnegie Institution of Washington Publication No. 389.*
By Harvey M. Hall. *Carnegie Institution*
$5.00 *Washington*
6$\frac{7}{8}$ x 10; viii + 391 (paper)

A taxonomic monograph attempting to classify a group of plants on the basis of their probable course of evolution. The author depends not only on field and herbarium studies but on experimental transplantation of diverse forms into a uniform environment. The conclusion is drawn that

> the species of North America have become definitely separated from those of farther south and that within each group there has been a development and differentiation which has led to the separation of smaller groups sufficiently distinct to be recognized as sections, 16 of these being in the north, 5 in the south. The nearest approach between sections appears to be between *Blepharodon* and *Euhaplopappus*, but even here the separation is based upon good technical grounds. It seems impossible, however, to set up any single character for the separation of all sections of North America from all those of South America, chiefly because of the numerous combinations in which the characters occur. It is for this reason that the primary geographic groups are not formally designated as subgenera.

ORGANOGRAPHIE DER PFLANZEN.

Insbesondere der Archegoniaten und Samenpflanzen. Erster Teil. Allgemeine Organographie.

By K. Goebel. *Gustav Fischer*
30 marks (paper) *Jena*
32 marks (cloth)
7 x 10¼; ix + 642

Goebel's *Organographie* is one of the great classics of biology. The first, general, part has long been out of print and this new third edition is therefore very welcome. The material has been thoroughly revised and brought up to date, additions having been made to practically all sections. A further long period of usefulness lies before the book.

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DIE KLIMATEN DES ERDBALLS UND DIE CHEMISCHE TÄTIGKEIT DER PFLANZEN.

By Sergius Ivanow. *Urban und Schwarzenberg*
4 marks 7 x 10; 39 (paper) *Berlin*

The point brought out in this number of the *Fortschritte der Naturwissenschaftlichen Forschung*, edited by Abderhalden, is that plants exhibit geographical variation in respect of their chemical constitution. This fact cannot be regarded as an entirely novel contribution, but the author brings a wealth of detail to its support, largely derived from his own studies of oil bearing plants in various parts of Russia and Siberia. The pamphlet is a curious and occasionally amusing mixture of sound and useful scientific information with Chamber of Commerce babbittry. The author lectures the Soviet Government at length about what they must do to promote a sound linseed oil industry for Russia.

LES PLANTES ALIMENTAIRES CHEZ TOUS LES PEUPLES ET À TRAVERS LES AGES. HISTOIRE, UTILISATION, CULTURE. *Volume II. Phanérogames Fruitières.*

By D. Bois. *Paul Lechevalier*
80 francs 6½ x 10; 638 (paper) *Paris*

This second volume, which completes Prof. Bois' valuable treatise on domesticated food plants, deals with the plants bearing edible fruits. It contains a wealth of information, covering a wide range beyond the directly botanical. It is copiously illustrated with line drawings, and will form a useful reference work in the agricultural and botanical fields. There is a detailed index.

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LA VIE DE LA CELLULE VÉGÉTALE.

Les enclaves de la matière vivante.

By Raoul Combes. *Armand Colin*
9 francs *Paris*
4½ x 6¾; 220 (paper)

The second volume in a planned trilogy on the plant cell. The first volume was noticed in this Review earlier (Vol. III, p. 296). The present volume is devoted to the subject of the vacuoles in plant cells, and their contents. It is a well-written, valuable book. The author is an uncompromising mechanist, bitterly opposed to the slightest and most innocent implication of teleology in biological discussion. He goes so far as to say that glycogen should not be called a "reserve substance," because to do so implies that the organism has an end in view. Rather glycogen should be called "a form of accumulation" of glucides. Such meticulous verbalism leaves us cold, though we appreciate the spirit which so stiffens one's backbone.

PLANT SUCCESSION AND INDICATORS. *A Definitive Edition of Plant Succession and Plant Indicators.*
By Frederic E. Clements.
The H. W. Wilson Co.
$8.50 6¾ x 9¼; xvi + 453 *New York*

This is a combined and condensed edition of the author's *Plant Succession* and *Plant Indicators* published in 1916 and 1920 by the Carnegie Institution of Washington. The portions of the original editions here omitted are to form the nuclei of three books, dealing with studies of succession in North America and Eurasia, with the new field of paleo-ecology, and with the climax formations of western North America.

The fundamental concept underlying Clements' work is that the unit or climax formation is an organic entity, which arises, grows, matures, and dies, whose "response to the habitat is shown in processes or functions and in structures which are the record as well as the result of those functions," and which is able to reproduce itself. All these are characteristic attributes of organisms. Clements traces the development of a sere or succession from a bare area, produced by various initial causes, through stages of migration of plants into the bare area, of adjustment and competition there, and of stabilization, to the climax stage, where "the occupation and reaction of a dominant are such as to exclude the invasion of another dominant." The second part of the book is built on the concept of plants, and especially plant communities, as indicators of soil and climate and therefore of the behavior of other plants and of animals in the same spot. There is a bibliography of 16 pages but no index.

This is an important ecological work, which fits in very neatly from the botanical side with Wheeler's concept of the society as the next emergent above the individual.

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DEUX ÉPIBIOTES REMARQUABLES DE LA MINGANIE. *Contributions du Laboratoire de Botanique de l'Université de Montréal—No. 12.*
By Frère Marie-Victorin. Laboratoire de Botanique, Université de Montréal
50 cents *Montreal*
6 x 9; 14 + 4 plates (paper)

LE DYNAMISME DANS LA FLORE DU QUÉBEC. *Essai sur les forces d'évolution et d'élimination en oeuvre dans certaines populations végétales. Contributions du Laboratoire de Botanique de l'Université de Montréal—No. 13.*
By Frère Marie-Victorin. Laboratoire de Botanique, Université de Montréal
$1.00 6 x 9; x + 89 (paper) *Montreal*

The first of these monographs deals with *Cypripedium passerinum* var. *minganense* and *Draba luteola*. The second is an interesting essay on ecological aspects of evolution. The author discusses especially the effect of man's activity on the flora of the earth, comparing its tendency to produce uniformity to the levelling effect of erosion.

* * *

FIELD BOOK OF AMERICAN WILD FLOWERS. *Being a Short Description of Their Character and Habits, a Concise Definition of Their Colors, and Incidental References to the Insects Which Assist in Their Fertilization.*
By F. Schuyler Mathews.
G. P. Putnam's Sons
$3.50 4 x 6¾; xxxii + 558 *New York*

A revised edition of a popular field book covering the flowering species of the eastern United States. A color key to assist in the identification of specimens as well as a family key and a general index are provided.

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THE GIANT CACTUS. *God's Monument to Faith, Patience and Perseverance.*
By Grace P. Nickerson. Trade Printing Co.
$1.00 6¼ x 10⅛; 29 *Los Angeles*

A brief, superficial but extremely enthusiastic account of these curious creatures of nature.

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DIE LEBENSDAUER DER PFLANZE.
By Hans Molisch. *Gustav Fischer*
7.50 marks (paper) *Jena*
9 marks (bound)
6¾ x 10⅛; viii + 168

An excellent and much needed treatise on the biology of life duration in plants, by the distinguished plant physiologist of Vienna. After an introductory chapter on duration of life, in general, in plants there are discussed means of prolonging the life of plants; rejuvenescence; latent life (*Scheintod*) in plants; and senescence, death and potential immortality of trees. There are author and subject indices. This will be a valuable reference work for all students of duration of life and related problems.

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HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 300.* Containing following articles: *Vom Sammeln und Präparieren der Kieselalgen sowie Angaben über Untersuchungs- und Kulturmethoden*, by Friedrich Hustedt; *Methoden zur Untersuchung der Kohlensäureassimilation*, by Hans Gaffron; *Methoden zum Nachweis pflanzlicher Wundhormone*, by Walter Kotte; *Neuere Methoden zur Ermittlung des Offnungszustandes der Stomata*, by M. G. Stalfelt.
Urban und Schwarzenberg
10 marks 7 x 10; 192 (paper) *Berlin*

Of general interest to botanists this number of the Abderhalden *Handbuch* contains, as its first article, the best account we have seen of all aspects of the technique of studying living diatoms.

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AGRICULTURAL AFGHANISTAN (*Composed on the basis of the data and materials of the Institute of Applied Botany to Afghanistan.*)
By N. I. Vavilov and D. D. Bukinich.
Institute of Applied Botany and State Institute of Experimental Agronomy
12 rubles 7 x 10⅛; 610 + xxxii *Leningrad*

A detailed report in Russian, with an extended summary in English, of an agricultural exploring expedition into Afghanistan, under the direction of the distinguished geneticist, Prof. Vavilov. Over 7000 samples of cultivated plants were collected, and tested out during three consecutive years in various parts of Russia. There are over 300 illustrations. These and the English summary are so interesting as to make one long to be able to read Russian, to get more of the details of this notable piece of biological exploration.

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TREES AND SHRUBS OF MINNESOTA.
By Carl O. Rosendahl and Frederic K. Butters.
University of Minnesota Press
$4.00 *Minneapolis*
6¾ x 10; viii + 385

A book which will give much pleasure to all those interested in the woody plants to be found not only within the boundaries of Minnesota but in the vast area extending from the Great Lakes to the Rocky Mountains. The authors have done their work with extraordinary care. Although designed primarily as a guide for the amateur and non-professional botanist the book meets all of the requirements of the serious student. Much material has been taken from the earlier work *Minnesota Trees and Shrubs* but the present volume is not simply a second edition of that treatise. It deals with native and introduced forms to the number of 47 families, 107 genera, 324 species, 40 varieties, 14 forms and 18 hybrids. The arrangement of families is according to the Englerian System, while in questions of nomenclature the International Rules as set forth by the Vienna Congress of 1905 and revised by the Brussels Congress of 1910 have been followed. An introductory chapter and glossary furnish the amateur with the necessary technical information. The book is beautifully printed and excellently illustrated with 250 figures and plates.

THE SCIENTIFIC PRINCIPLES OF PLANT PROTECTION.

By Hubert Martin. Longmans, Green and Co.
$8.40 5¾ x 8½; xii + 316 *New York*

The primary object of this book is to make "a comprehensive survey of the scientific principles underlying modern methods of control of crop pests" as an aid in the ever increasing necessity for cooperation between the entomologist or mycologist, on the one hand, and the chemist, physicist or plant physiologist, on the other. The author deals clearly and in detail with the diverse aspects of the problem: chemical and physical modes of attack by fumigating or spraying with insecticides or fungicides; the treatment of soil and seed by chemicals; the use of insects, fungi or bacteria as enemies of plant parasites; selecting and breeding disease resistant strains; etc. The book is well documented and has author and subject indices.

THE HYDROSTATIC-PNEUMATIC SYSTEM OF CERTAIN TREES: MOVEMENTS OF LIQUIDS AND GASES.

Carnegie Institution of Washington Publication No. 397.
By D. T. MacDougal, J. B. Overton and Gilbert M. Smith. *Carnegie Institution*
$1.25 *Washington*
6⅞ x 10; 99 (paper)

A further report on the important experimental researches of MacDougal and his associates on the movement of water in trees. The first conclusion reached is that: "Our experiments show that the living cells of the stem have no active rôle in sap-flow other than their effect upon the osmotic concentration of the transpiration stream." This volume is a contribution of first rate importance to the literature of plant physiology.

MORPHOLOGY

VERGLEICHENDE ANATOMIE DES NERVENSYSTEMS DER WIRBELLOSEN TIERE. *Unter Berücksichtigung Seiner Funktion.*

By Bertil Hanström. *Julius Springer*
76 marks (paper) *Berlin*
78.60 marks (cloth)
7 x 10; xi + 628

A thorough, detailed, and comprehensive review of the existing knowledge of the nervous system in invertebrates, with a strong flavor of emphasis on the functional aspects throughout. The book is abundantly and well illustrated; is thoroughly documented, though it is questionable if it would not have been more practically useful to have collected together in one place all the bibliographies which are scattered through the book after each chapter; and is fairly well indexed. It constitutes a valuable reference work in its field.

ENTWICKLUNGSGESCHICHTE DES MENSCHEN *mit Berücksichtigung der Wirbeltiere.*

By Richard Weissenberg. Originally by L. Michaelis. *Georg Thieme*
10.70 marks *Leipzig*
5⅛ x 7¾; xii + 293 + 6 plates

So successful has this handbook of human embryology been that Professor Weissenberg now issues a new and enlarged eleventh edition, with his name appearing as the primary author. Within its brief limits it is one of the best available summaries of what is known about the embryonic development of the vertebrate body in general and the human body in particular. It is well illustrated and indexed.

COMPARATIVE NEUROLOGY. A *Manual and Text for the Study of the Nervous System of Vertebrates.*

By James W. Papez. *Thomas Y. Crowell Co.*
$6.00 5¾ x 9; xxv + 518 *New York*

An introductory laboratory course divided into three parts: I. Gross Structure of the Brain of Mammals; II. Microscopic Structure of the Mammalian Nervous System; III. Brains of Lower Vertebrates. It is amply supplied with diagrammatic drawings and contains lists of references.

COMPTES RENDUS DE L'ASSOCIATION DES ANATOMISTES. *Vingt-troisième Réunion (Prague, 2–4 avril 1928).*

Edited by Remy Collin.
L'Association des Anatomistes,
11 francs in France *Faculté de Médecine*
12 francs in foreign countries *Paris*
6½ x 9¾; lii + 559 (paper)

This volume of the proceedings of the 1928 meeting of the French Association of Anatomists contains some 91 papers, many of real interest and novelty, besides the minutes of the meeting.

LEHRBUCH DER ENTWICKLUNG DES MENSCHEN.

By Alfred Fischel *Julius Springer*
86 marks (paper) *Berlin*
88.80 marks (bound)
6¾ x 10⅛; viii + 822

A detailed and thorough textbook of human embryology, extensively and beautifully illustrated. It is a textbook in the strictest sense. There are no bibliographical citations whatever, except that borrowed figures are credited to the original author, but without citation of place of publication. Here is set down, in excellent order and thoroughness of detail, that which needs to be learned by the student of the development of the human body. The book is well indexed. But indubitably its value as a *reference* work is diminished by the absence of a bibliography.

A COURSE IN COMPARATIVE ANATOMY. In four volumes, as follows: *Outline Lectures in Comparative Anatomy and Vertebrate Zoölogy; The Dissection of the*

Dogfish; The Dissection of the Turtle; The Dissection of the Toad with Remarks on the Anatomy of the Frog and the Salamander.
By Edwin C. Starks and Lot D. Howard.
Stanford University Press
$3.00 per set *Stanford University*
6 x 8¾; I, 49 (paper)
II, 36 (paper)
III, 36 + 2 plates (paper)
IV, 34 + 2 plates (paper)

A didactic outline of lectures for an elementary course in comparative anatomy and three laboratory manuals for the dissection of the dogfish, turtle and toad. There is a short list of references supplied with each part.

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ÉLÉMENTS D'HISTOLOGIE. *I. Cellule. Division cellulaire. Différenciation cellulaire. Classification morphologique et fonctionnelle des cellules, tissus et organes. Éléments de soutien, contractiles, nutritifs. Sang, lymphe, organes hématopoïétiques, vaisseaux sanguins et lymphatiques.*
By P. Bouin. *Félix Alcan*
120 francs *Paris*
8⅝ x 10⅝; vii + 334

This first volume of a new and comprehensive textbook of histology, by the great French master in that field, Professor Bouin, is concerned with the cell in general, the problem of differentiation, and cell physiology. The orthodox plan of arranging treatises on histology on the basis of tissues and organs is here wholly abandoned, and replaced by the more logical plan of treating together those basic cellular elements which play a common rôle. The whole outlook of the book is fresh and stimulating. It is beautifully printed and illustrated. Following each chapter is a selected, but rather extensive, bibliography. The whole work, when completed, will take rank as a standard text and reference book.

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CONTRIBUTIONS TO EMBRYOLOGY. *Volume XX, Nos. 109 to 117. Publication No. 394.*
Carnegie Institution of Washington
$5.50 (paper) *Washington*
$6.50 (cloth)
9 x 11¾; 257

This volume contains the following contributions: Early stages in the development of pig embryos, from the period of initial cleavage to the time of the appearance of limb-buds, by C. H. Heuser and G. L. Streeter; The development of the meninges in amphibia: a study of normal and experimental animals, by Louis B. Flexner; On the placentation of primates, with a consideration of the phylogeny of the placenta, by G. B. Wislocki; A well-preserved human embryo of 10 somites, by George W. Corner; The topographic history of the volar pads (walking pads; *Tastballen*) in the human embryo, by Harold Cummins; A correlated study of the development of reflex activity in fetal and young kittens and the myelinization of tracts in the nervous system, by Orthello R. Langworthy; The effect of various solutions and salts on the pulsation rate of isolated hearts from young chick embryos, by Warren H. Lewis; Macrophages and other cells of the deep fascia of the thigh of the rat, by Warren H. Lewis; The technique of measuring the outer body of human fetuses and of primates in general, by Adolph H. Schultz.

The usual high standard of excellence associated with the work of the Carnegie Institution Department of Embryology is well maintained in this volume, both as to matter and method of presentation.

PHYSIOLOGY AND PATHOLOGY

THE COMPARATIVE PHYSIOLOGY OF MUSCULAR TISSUE.

By A. D. Ritchie. *The Macmillan Co.*
$3.00 5½ x 8½; xi + 111 *New York*

A valuable contribution to this special field. There are four general headings: General characters of muscular tissue; chemical changes in active muscle; mechanics and theory of muscular contraction; and effect of environment. The author is led by his own researches and an extensive review of the literature to the conclusion that so far as evidence goes the mechanism underlying the simple muscle twitch is sufficient to explain all muscle processes. The difference between muscles seems to be in the speed of the processes rather than in their quality. The book is well documented and indexed.

A REPORT OF EXPERIMENTS INDICATING SOME NEW FACTORS IN RESPIRATION. *University of Toronto Studies. Physiological Series No. 98.*

By E. Fidlar. *University Library*
50 cents 6¼ x 9¾; 77 (paper) *Toronto*

The detailed report of an extremely interesting and ingenious piece of physiological research, leading to the conclusion that in the respiration of frogs in a closed circuit there is evidence of "the presence of unknown gas or gases, assumed 'nitrogen,' not only as an excretion of the animal, but also as an absorption, and in the two most accurate experiments the ratio of outgo to uptake was about 2:1."

WHEAT FLOUR AND DIET.

By C. O. Swanson. *The Macmillan Co.*
$2.50 4⅞ x 7⅞; xiii + 203 *New York*

This book is written for the general reader. Teachers of home economics, diet and nutrition, and milling processes, however, will find it useful. Its aim is to give, in non-technical language, the different operations involved in the complex process of making wheat flour. In addition, there is an account of the development of the milling industry, which had its origin long before written history, a chapter on vitamines, and a discussion of the importance and uses of the various types of wheat. Considerable space is devoted to the value of wheat flour in the diet and to the general relations of food to health. This latter part is particularly sound and satisfying when one considers the great mass of half-baked and dubiously seasoned food-lore which of late has been so frequently dished up for the general reader's diet. The illustrations are well chosen.

DAS PERMEABILITÄTSPROBLEM. *Seine Physiologische und Allgemeinpathologische Bedeutung.*

By Ernst Gellhorn. *Julius Springer*
34 marks (paper) *Berlin*
35.40 marks (cloth)
5¾ x 8¾; x + 441

A useful critical review of the literature, to the middle of the year 1928, on permeability, together with some original experimental work of the author in this field, not published elsewhere. The bibliography is colossal, running to about 1400 titles. The main topics discussed are the methodology of experimental work on permeability; the permeability of the cell; and the permeability of organs. These sections are followed by a general summary and synthesis of results.

LA VACCINATION ANTITUBERCULEUSE AVEC LES BACILLES VIVANTS CHEZ LES ANIMAUX ET CHEZ L'HOMME. *By Alberto Ascoli, in collaboration with E. Gentili, G. Gerosa, A. Mangiarotti, D. Nai, C. Setti, F. Omodeizorini.*
Istituto Editoriale Cisalpino
6¼ x 9⅛; iii + 235 (paper) *Milano*

An account of the author's own researches, with a historical setting, and much discussion of Calmette's BCG work. The book is chiefly of interest to the clinician and public health worker, rather than the biologist. It unfortunately lacks an index.

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FOOD, NUTRITION AND HEALTH.
By E. V. McCollum and Nina Simmonds.
E. V. McCollum
East End Post Station Box 25,
$1.60 4⅞ x 7½; vii + 148 *Baltimore*

A revised second edition of a popular treatise on the results of modern research on food and nutrition. The book contains much that is sound and interesting, especially in those chapters dealing with the vitamines. Its greatest value is perhaps to a somewhat specialized group—the physician, the dentist, the dietitian and the nurse. As no modern popular treatise of this kind is complete without aids to reducing or increasing the body weight, so we find the latter third of the book devoted to such suggestions, together with a "system of diet promoting health."

* * *

TRACKING DOWN THE ENEMIES OF MAN. *Being the Romance of a Doctor's Life in the Jungles.*
By Arthur Torrance. *J. H. Sears and Co., Inc.*
$3.50 5½ x 8⅛; xiii + 296 *New York*

This somewhat lurid book is launched by Trader Horn and Morris Fishbein. It recounts various adventures of the author in the course of his medical service and experience in the tropics. It is highly entertaining reading though of no scientific significance.

* * *

DIE MALARIA *in ihrer Bedeutung für die Geschichte Roms und der römischen Campagna. Eine kulturhistorische Studie.*
By Angelo Celli (Edited by Anna Celli-Fraentzel, with a foreword by Henry E. Sigerist). *Georg Thieme*
12 marks *Leipzig*
6½ x 9¾; vi + 118 (paper)

It is a real service to have this renowned essay of Celli available in German. It is a thorough historical study of the epidemiology of malaria in the Roman *campagna*, thoroughly documented, and makes a fundamental contribution to human biology in general, as well as to epidemiology in particular.

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HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 288.* Containing following articles: *Ein transportabler Respirationsapparat für medizinische, anthropologische und andere wissenschaftliche Expeditionen: Ein einfacher adiabatischer Calorimeter zur Bestimmung der Energiewerte von Brennstoffen, Nahrungsmitteln und Exkreten;* and *Der Oxycalorimeter*, by Francis G. Benedict.
Urban und Schwarzenberg
4 marks 7 x 10; 80 (paper) *Berlin*

Lieferung 293. Methoden und Technik der Nerven- und Muskelphysiologie bei wirbellosen Tieren.
By H. J. Jorden and P. J. van der Feen
Urban und Schwarzenberg
8 marks 7 x 10; 143 (paper) *Berlin*

Lieferung 296. Containing the following articles: *Methoden zur experimentellen*

Schädigung des Gehörorgans durch Schalleinwirkung, by Carl v. Eicken; *Elektrische Methoden zur Klanganalyse*, by Ferdinand Trendelenburg.

Urban und Schwarzenberg
6 marks 7 x 10; 99 (paper) *Berlin*

These three numbers of the Abderhalden *Handbuch* are of special interest to physiologists. The first by Dr. Benedict, director of the Carnegie Institution's Nutrition Laboratory, is especially important because it describes extremely neat and compact pieces of apparatus, by means of which metabolism may be studied in the field.

ÉTUDE ÉLÉMENTAIRE DES ARYTHMIES. *Lecture des Éléctrogrammes Phono et Cinématographie.*

By R. Lutembacher. *Masson et Cie*
30 francs *Paris*
7⅝ x 10½; 110 (paper)

A beautifully illustrated treatise on electrocardiography, with especial reference to pathological disturbances of the cardiac rhythm. The different common cardiac lesions are discussed and electrocardiograms illustrating them are reproduced. There are also examples of microcinematography.

FUNGI AND FUNGOUS DISEASES (*Adolph Gehrmann Lectures of the University of Illinois College of Medicine 1926*).

By Aldo Castellani. *American Medical Assoc.*
$1.50 6⅞ x 10; 203 (paper) *Chicago*

Three lectures by the noted authority on Tropical Diseases: I. Fungi; II. Fungous Diseases; III. Skin Diseases Due to Fungi.

NOMENCLATURE *of Diseases and Operations and Manual of the Medical Record.*

By T. R. Ponton. *Physicians' Record Co.*
$3.50 6¼ x 9½; 199 *Chicago*

Alphabetical list of some 24,000 diseases according to a nomenclature approved by the American College of Surgeons and the American Hospital Association. Each disease has a number for use in punch card index systems, and a letter designation to facilitate the assignment of cases to different hospital departments. There are also a list of surgical operations and sample hospital records.

THE GENESIS OF EPIDEMICS *and The Natural History of Disease. An Introduction to the Science of Epidemiology Based upon the Study of Epidemics of Malaria, Influenza, and Plague.*

By Clifford A. Gill. *William Wood and Co.*
$7.50 5¾ x 9; xxvi + 550 *New York*

This is an exceedingly well reasoned inquiry into the basic nature of the etiology of epidemics. The author, who is Director of Public Health in the Punjab, has had an extensive experience with epidemic disease in the field and tells of the origin of the present work. Having been engaged in the study of malaria in the Punjab continuously from 1913 to 1923 and for some years again after an interruption by the war, he published a definitive paper in 1921 stating provisionally the hypothesis which appeared to him to account for the malarial outbreaks. Later, taking up other epidemics for their bearing on his malarial work he was impressed with the similarity of all epidemical phenomena and in 1922 a generalization applicable to all epidemics of disease was adopted. It is thus seen that the author's theory has the merit of having been inductively developed, and following this it was tested by application to influenza, plague, and certain other diseases with such satisfactory results that a complete synthesis was undertaken.

The presentation is arranged in five parts. The first, an introductory one, defines an epidemic as a sharp increase in incidence over a short period of time, and epidemicity is defined dynamically to refer to "those qualities affecting the seed and the soil whereby certain diseases are enabled periodically to exhibit epidemical phenomena." It then recounts the previous views regarding the cause of epidemics, outlines the objects of epidemiological research and gives a brief statement of the author's theory of the genesis of epidemics. Part II is devoted to the results of an investigation of epidemic malaria and an account of studies of influenza and plague. Part III is an analysis of an application of the author's theory of epidemics. Part IV contains a discussion of the influence of evolutionary factors on disease and the effect of climate. Part V is a review and reflects on the implications of the author's views for the theory and practice of preventive medicine.

Colonel Gill calls his hypothesis the "quantum theory," and it is a generalization applying to all epidemics in spite of the apparent disparate character of epidemics of different diseases. Instead of attributing epidemics to changes in an individual factor, such as the biological modification of the specific parasite, which is the prevalent view, the author proposes the idea that they arise as a result of the disturbance of a quantitative equilibrium between toxin and degree of immunity. A number of influences may bring about such a disturbance and four factors are emphasized: (1) the reservoir of infection, (2) the parasite factor, (3) the immunity factor, and (4) the transmission factor. The factor of predominating importance is the one of transmission, and this in turn is largely affected by meteorological conditions. The theory is presented with great skill, and much evidence, which there is no space available here to review, is educed in its favor. Whether or not it eventually stands, Colonel Gill has produced a great work on epidemiology as lucidly written as it is well conceived.

BIOCHEMISTRY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 287.*

Containing following articles: *Sulfonieren*, by Josef Halberkann and Fritz Fretwurst; *Biologisch wichtige Reaktionen und Reagenzien*, by Eduard Strauss and Karl Koulen.

Urban und Schwarzenberg
10 marks 7 x 10; 180 (paper) *Berlin*
Lieferung 294. Darstellung metallorganischer Verbindungen.
By Emil Klarmann. Urban und Schwarzenberg
8 marks 7 x 10; 158 (paper) *Berlin*
Lieferung 299. Halogenieren.
By Hugo Bauer. Urban und Schwarzenberg
14 marks 7 x 10; 276 (paper) *Berlin*

The articles in these three numbers of the great Abderhalden *Handbuch* are chiefly of interest to biochemists. The one by Strauss and Koulen on biologically important reactions and reagents is of general biological interest and usefulness.

THE CHEMICAL ACTION OF ULTRA-VIOLET RAYS.

By Carleton Ellis and Alfred A. Wells.
The Chemical Catalog Co., Inc.
$6.50 6 x 9; 362 *New York*

A summary and not very searching

account of some of the chemical and biological uses of ultra-violet radiation.

ENZYME ACTIONS AND PROPERTIES.

By Ernst Waldschmidt-Leitz. Translated and Extended by Robert P. Walton

John Wiley and Sons, Inc.
$4.00 net *New York*
$5\frac{3}{4}$ x 9; xviii + 255

"The material within this volume constitutes a general treatment of enzyme action and properties as interpreted principally from the viewpoint of the Willstätter school. Prof. E. Waldschmidt-Leitz, the active associate of R. Willstätter, has given a condensed description of the most important principles of enzyme chemistry and of the special characteristics of the most prominent enzymes. The work has not been attempted as an exhaustive compendium of enzyme literature but rather as a concise presentation of the most fundamental principles and best accepted characteristics of enzyme action."

THYROXINE.

By Edward C. Kendall.

The Chemical Catalog Co., Inc.
$5.50 6 x 9; 265 *New York*

The scope of this monograph, the forty-seventh in the authoritative series issued by the American Chemical Society, is indicated by the following extracts from the preface.

> What has been assembled in the monograph has been chosen from the viewpoint of a chemist and with a desire to correlate the activity of the thyroid gland with reactions which involve oxidation. . . .
>
> The theoretical deductions in this monograph have been largely based on three contributions: the clinical classification of goiter and the use of iodine in exophthalmic goiter which have been suggested by Plummer: the isolation of thyroxine from the gland; and the extensive studies in basal metabolism and nitrogen metabolism in relation to thyroxine and thyroid diseases which have been carried out by Boothby and his coworkers. . . .
>
> The experimental results to which reference has been made have been limited to those that establish the physiologic activity of thyroxine and those necessary to relate the action of the thyroid gland to the normal physiology of the human being.

SEX

A RESEARCH IN MARRIAGE.

By G. V. Hamilton.

Albert and Charles Boni, Inc.
$10.00 6 x 9; xiii + 570 *New York*

WHAT IS WRONG WITH MARRIAGE.

By G. V. Hamilton and Kenneth MacGowan.

Albert and Charles Boni, Inc.
$3.00 $5\frac{1}{2}$ x $8\frac{5}{8}$; xxi + 319 *New York*

The investigation of sex life and marriage which forms the basis of these two books deserves attention and commendation as a pioneer effort in an important but too much neglected field of human biology. It is easy to criticise specific weakness in Dr. Hamilton's work, and this has been rather freely done. But really pioneer work in any field of science is only rarely perfect.

Dr. Hamilton, in the following statement, makes clear in general terms the nature of his material and of the investigation as a whole.

> An almost freakish combination of circumstances made it possible for me to obtain intimate and extensive self-revelations from two hundred married persons who are serious-minded, more or less importantly occupied and well above the average as to intelligence and cultural attainment. At least half of them could be rated as "normal" in the sense that their spousal, parental, social and vocational adjustments conform to standards which are not exceeded by the majority of Americans. Nevertheless, it would be over-optimistic to say that as many as five per cent of them

> have escaped more or less serious damage by preventable things which were done to them during childhood. This book presents (1) some of the more important things that happened to the two hundred spouses of my study during their childhood, and (2) their present beliefs, attitudes, predicaments, and characteristic modes of performance with reference to sex and marriage. It is therefore in a measure a study of the child in the adult.

The actual technique was, in briefest outline, to place each subject in a comfortable chair in Dr. Hamilton's office and present the person with library cards, one by one, on each of which was typed one or more questions about their sex life, in nearly all the aspects conceivable. Dr. Hamilton sat quietly at his desk and wrote down the answers, as they were freely "talked out."

The book is devoted to detailed compilations (or really lists in many cases) of the answers to these questions. Quite intentionally, whether wisely or not, the result is of the nature of a large collection of trees, rather than a forest. Dr. Hamilton is very modest throughout, and refrains from drawing any general conclusions. In spite of the inevitable defects of a first trial the book is a notable contribution.

The second book is a popular presentation of some of the material, for general circulation. The *Research in Marriage* is prohibited from circulation except among the members of certain professions.

THE INVERT *and his Social Adjustment.*

By Anomaly. *The Williams & Wilkins Co.*
$2.00 4 x 6½; xxxii + 160 *Baltimore*

This interesting little book may be described as a sort of handy guide or *vade mecum* for the homosexual desirous of keeping out of jail. These unfortunate persons have a difficult time adjusting themselves in a world run by and for heterosexuals. The author is a Roman Catholic, and has derived help from that source in his difficulties. He ends on an optimistic note. "I predict that the next decade will witness a better understanding of the facts of inversion by all educated people, and better understanding will relieve inverts from much of the present necessity for dissimulation."

On the whole, we suspect that this book will be found very helpful by the intelligent, high-toned invert; and it will certainly help other people to gain an understanding of his point of view. But what a pity it is that there is a biological necessity for such a book to be written! Only the dialectical agility of a Dr. Pangloss can produce satisfaction out of so grievous a cosmic biological error.

INFLUENCES SOLAIRES ET LUNAIRES SUR LA NAISSANCE HUMAINE.

By K. E. Krafft. *Norbert Maloine*
8 francs 5½ x 9; 50 (paper) *Paris*

A contribution to astrobiology. The author is no mere theorizer, but a hard working statistician. No small amount of statistical drudgery went into this volume. Mr. Krafft believes that influences of cosmic origin, reflected in the position of sun, moon, and stars, have a profound influence upon human biological events upon the earth. This particular essay deals with the sex ratio from that point of view. The sun plays the more important rôle in male births and the moon in female. We commend the book to the attention of statisticians.

WHAT EVERYBODY WANTS TO KNOW. *The story of sex-appeal with a complete and scientific course of exercises*

designed to build health and to give you that attraction which is the basis of love and marriage.
By Lilyan I. Malmstead. *Morning Glory Products*
$3.00 *Worcester, Mass.*
6 x 7½; 128

A system of exercises and diet which, coupled with the assiduous use of "Morning Glory" moulding cream and astringent and the wearing of the "Morning Glory Step-in Girdle," is guaranteed to produce and maintain IT. Photographs of Lilyan (herself) illustrate the treatise, and there is no denying that she is restful to the eye, though Reginald, the Office Boy, says he doesn't see why she has to have on the "Morning Glory Step-in Girdle" in *every* picture. IT, we are told, is and always has been, "sex appeal." While the book strenuously devotes itself to plain and simple instruction about how to get and hold this desirable quality, nevertheless its morals are beyond reproach. "Sex should never be dissipated by promiscuity nor put up for sale" says she.

* * *

WHY WE ARE MEN AND WOMEN *or Factors Determining Sex.*

By A. L. Benedict. *Allen Ross and Co.*
$2.50 net 5 x 7⅜; 274 *New York*

This book has been written for the general reader. A great amount of scientific, pseudo-scientific, and other rather dubious material on sex determination has gone into the making of it. No doubt some readers will feel that they are acquiring a vast amount of knowledge hitherto withheld from them, but, critically considered, it is an example of the kind of popularization of science which grieves the judicious.

BIOMETRY

FORECASTING WHEAT YIELDS FROM THE WEATHER. *Elements of an Unsolved Problem. Wheat Studies of the Food Research Institute, Vol. V, No. 1.*

Food Research Institute
$1.00 *Stanford University*
8½ x 11; 44 (paper)

A timely discussion of an important problem which up to the present has been attacked by subjective rather than objective methods. Under the following headings are presented the status of the problem and lines of attack upon this increasingly bewildering phase of agricultural economics. Preliminary considerations; weather factors in plant growth; plant reactions to weather factors; some interrelations of growth factors; methods of forecasting yields from the weather; pitfalls of correlation analyses; present results and lines of improvement; bibliography.

The conclusion is reached that the main improvement in forecasting will probably come from controlled laboratory and field experiments concerning the reaction of crops to various weather factors. Too little attention has heretofore been paid in forecasting to the plant as a reacting organism. The ultimately successful solution of the problem is only possible by the coöperation of meteorologists, agronomists, physiologists, pathologists, and entomologists, working over a period of many years with improved or modified methods in each of these lines of work.

* * *

NOMOGRAPHIE.

By M. Fréchet and H. Roullet. *Armand Colin*
9 francs (paper) *Paris*
10.25 fr. (cloth)
4½ x 6¾; 208

A useful elementary treatise on graphical computation, written by a mathematician and an engineer in collaboration. It ranges both wider and deeper than Brodetsky's comparable volume on the same subject. It is clearly and simply written.

PSYCHOLOGY AND BEHAVIOR

ANATOMY AND THE PROBLEM OF BEHAVIOUR.

By G. E. Coghill. *The Macmillan Co.*
$3.00 $5\frac{3}{8}$ x $8\frac{1}{2}$; xii + 113 *New York*

In the course of three lectures given at University College, London, the author presents his interesting and highly important work on the correlation of the structural development of the nervous system with the development of behavior. The work was chiefly upon *Amblystoma*, which in many respects is an ideal organism for such experimental studies.

Lecture I deals with the development of the behavior pattern in *Amblystoma* and the nervous mechanism which forms a basis for such a pattern. The following summary is given:

> The behavior pattern develops in a regular order of sequence of movements which is consistent with the order of development of the nervous system and its parts: in a relatively precise manner physiological processes follow the order of their embryological development in the functions of aquatic and terrestrial locomotion and feeding: behavior develops from the beginning through the progressive expansion of a perfectly integrated total pattern and the individuation within it of partial patterns which acquire various degrees of discreteness.

That the nervous mechanisms have their origin in the functions and structures of early embryonic life is the thesis of his second lecture. In the embryo, before the neural processes have appeared, there is complete integration within the tissues brought about by a coördination of the processes of growth. Many amphibia exhibit a coördination of the ectodermal cilia, causing a constant movement within the egg membrane. The paths of the nervous system are "blazed" in the early embryonic stage, the preneural pattern of localized centers determining where the differentiation of nerve cells shall occur later. The hypothesis is offered that "a gradient of electric potential acting along the external limiting membrane is the essential factor in determining the path along which the nascent nerve cell shall grow." The gap between the early non-nervous condition of the embryo where there is already perfect integration and the later stage where the nervous system appears is merely superficial. There is, in fact, an overlapping of the preneural system of integration upon the neural in the regular course of development, and this overlapping is highly significant in interpreting the development of behavior in the organism.

In the third and last lecture the author "shows how the preneural process of growth and differentiation in the nervous system, and particularly in the individual nerves, participates in the function of the nervous system as a whole."

There is a bibliography of two and a half pages, but no index. This is an important book.

CHIMPANZEE TRANSLOCATION BY MEANS OF BOXES. *Comparative Psychology Monographs Vol. 5, No. 3, Serial No. 25.*

By Harold C. Bingham.
The Johns Hopkins Press
$1.75 7 x $10\frac{1}{4}$; 91 (paper) *Baltimore*

An account of experiments in stacking boxes to reach a lure under more controlled conditions than in the similar experiments of Yerkes and Köhler. Evidence is found of ideational behavior.

THE BATTLE OF BEHAVIORISM. *An Exposition and an Exposure.*

By John B. Watson and William MacDougall. *W. W. Norton and Co., Inc.*
$1.00 4¼ x 6½; 96 *New York*

The debate over behaviorism before the Psychological Club of Washington in 1924 is now published in Norton's "New Science Series," with a postscript by MacDougall, in which he takes the opportunity "to draw the attention of readers of this booklet to several of my more recent publications on this topic." In spite of a natural sympathy with Watson as the victim of MacDougall's forensic tricks, we cannot help doubting whether, in a world where even the electrons are coming to have a purpose, he will succeed in keeping purpose out of psychology.

THE MIND OF A GORILLA. *Part III. Memory. Comparative Psychology Monographs Vol. 5, No. 2.*

By Robert M. Yerkes. *The Johns Hopkins Press*
$1.75 7 x 10¼; 92 (paper) *Baltimore*

This is the third and final report by Professor Yerkes on his remarkably interesting series of studies on the mental and physical development of the captive female gorilla, Congo. It is most unfortunate that the experimenter could not have carried out his plan of spending some weeks each year in following her development to maturity. The death of Congo, due apparently to acidosis, secondary to ileocolitis, occurred in April, 1928. Studies made on her skeleton indicate that she was approximately eight years old. The rate of growth which different portions of the gorilla's body exhibited was exceedingly irregular. At one time the lower extremities would grow with greater rapidity—at another, the head or upper extremities. Regarding the psychobiological development and status the author states that

> The subject continued to exhibit in increasing variety, and especially in affective attitude and aspects of adaptivity, indications of transition from childhood to early maturity. Behavior suggested adolescence, but this was not definitely confirmed by physical status. Naïveté and the inhibitions due to timidity and lack of confidence gradually and increasingly gave place to such freedom and assurance of action as in human life indicate familiarity, experience, wisdom.

There was indication that experience gained in solving problems previously presented to her was transferred, in part, at least, to the solution of new problems and situations. There was lack of curiosity and desire to imitate. She never exhibited violent emotions. In sharp contrast to man and chimpanzee the investigator found Congo "slow in sensory reaction, perception, discrimination, decision, ideation (or their physiological equivalents), and in behavioral adaptation." Although there was no evidence that the menstrual periods had been established her sexual behavior and sex play indicated that she was in the adolescent stage of development and approaching sexual maturity.

THE PSYCHOLOGY OF LANGUAGE.

By Walter B. Pillsbury and Clarence L. Meader. *D. Appleton and Co.*
$3.00 5⅛ x 10; ix + 306 *New York*

This book, by two distinguished scholars, is the logical outgrowth of the development of researches along two lines

—on the one hand, a study of psychology so far as it bears on language, and, on the other hand, a study of the origin, growth and interrelations of languages. The development of the intricate articulate movements of speech from the primitive so-called vegetative processes of the organism is traced and the relation of thought and emotion to those same physiological processes. The psychological interpretation of language based on a study of the science of phonetics and linguistics is discussed. There are many interesting sections throughout the book, among which may be mentioned the discussions of the origin and movements of articulation, the primitive forms of memory, the process of learning and the Morse Code, and the real distinction between word and sentence.

ANIMAL PSYCHOLOGY FOR BIOLOGISTS.

By J. A. Bierens de Haan.

University of London Press, Ltd.
4 s. 6 d. net 5½ x 8½; 80 *London*

This little book contains three lectures given at King's College, University of London. It is an interesting and stimulating presentation of a point of view regarding animal psychology which seems to us to be sound and useful. The author feels that the extreme "behaviorist" and the extreme anthropopsychic positions are equally to be condemned as philosophical guides to the actual investigation of animal psychology. He believes that higher animals (for example, dogs) have a "kind of practical intelligence, an understanding of the relations of things and an insight into the results of their actions which is sufficient for the needs of practical life." There is a bibliography covering three pages, but no index.

MODERN PROGRESS IN ZOOPSYCHOLOGY (*In Russian*).

By D. N. Kashkaroff.

Soviet Government Printing Office
3.75 roubles *Leningrad and Moscow*
5¾ x 8¾; 425

The book represents a very thorough and critical survey of the field of modern psychology of animals, or the science called in the United States "behaviorism." The author is a great admirer of American experimental methods as applied to the study of animal psychology. In the preface he expresses the opinion that it is only thanks to these new ideas and methods that the position of zoopsychology has found its justification among other biological sciences. More than three hundred special papers are cited in the list of literature, of which nineteen only are original Russian ones. The majority of those in foreign languages belong to American authors. The book will certainly open a new period of acquaintance of Russian reading circles with the progress of exact psychology in America. So far as we know, no other European country contains such a splendid review of the brilliant modern American zoopsychological movement.

BIBLIOGRAPHY OF RESEARCH STUDIES IN EDUCATION 1926–1927.

Department of the Interior Bureau of Education Bulletin No. 22.

By John D. Wolcott.

U. S. Government Printing Office
25 cents *Washington*
5⅞ x 9¼; vii + 162 (paper)

Lists 1540 researches in education published in the United States during the year ending June 30, 1927. An author and subject index and one of institutions are supplied.

ADAPTIVE MOTOR HABITS OF THE MACACUS RHESUS UNDER EXPERIMENTAL CONDITIONS. *A Contribution to the Problem of "Labour Processes" of Monkeys.*

By N. Kohts. Zoopsychologisches Laboratorium am Museum "Darwinianum."

7.50 rubles *Moscow*

7 x $10\frac{3}{4}$; 368 (paper)

A detailed account in Russian of an extensive experimental research on the behavior of the monkey. There is a summary in English covering 27 pages. The distinguished authoress is of the opinion that the macaque is a product of regressive evolution "down from better developed ancestors." He is, as he exists today, incapable of work, in the human sense. The volume is illustrated with 24 plates and 67 text figures. It is a contribution of first rank importance to the study of animal behavior and psychology.

* * *

THE GROUP MIND. *A Sketch of the Principles of Collective Psychology with Some Attempts to Apply Them to the Interpretation of National Life and Character.*

By William McDougall. G. P. Putnam's Sons

\$3.50 $5\frac{1}{4}$ x $8\frac{1}{2}$; xxx + 418 *New York*

This is the second edition of McDougall's well known book. The author notes that some recent expressions of scientific thought such as that of the *Gestalt* psychologists and the Holism of General Smuts support his idea of the Group Mind as a valid scientific entity, though it is still depreciated by most psychologists. We think ourselves that the fundamental notion is less dubious than the elaboration in the text. Of his subject the author remarks: "For to the obscure questions of fact with which he deals, it is in the nature of things impossible to return answers supported by indisputable experimental proofs." Perhaps that puts as well as may be the weakness from which his conclusions suffer.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

DECIMALISM *or Progressive Selection. Aristocracy and Democracy transcribed in a fantasia of Common Sense. Offered seriously to those who when the wind is southerly know a hawk from a handsaw.*

By A Citizen of No Importance.

Richard G. Badger

\$1.00 5 x $7\frac{1}{2}$; 75 *Boston*

This is an interesting little tract, which is worth reading in spite of its bizarre title, and unconventional spelling. The idea of the book is the not entirely novel one that this might be a better country to live in if the method of choosing the people to run the government, local and national, were altered to something totally different from what it now is. There is a good deal of trenchant and sensible criticism in the book, and the author's panacea is not bad, on paper. But it has about as much chance of being adopted as a hawk has to become a handsaw, to change the author's pleasant alliteration.

* * *

THE TURNING POINT. *A Revised Edition.*

By Richard J. Flanagan.

Perry and Elliott Co.

5 x $7\frac{3}{4}$; 77 (paper) *Boston*

Once more our friend opposed to excess in the drinking of water comes to the fore (see QUARTERLY REVIEW OF BIOLOGY, Vol. III, p. 598). He has enlarged and, in unimportant ways, altered his dissertation on the subject.

THOMAS HOBBES' MECHANICAL CONCEPTION OF NATURE.

By Frithiof Brandt. *Librairie Hachette*
18 shillings (paper) *London*
21 shillings (cloth)
7 x 10½; 399 (paper)

This thorough analysis of the writings of Thomas Hobbes was originally published in Danish in 1921, as the author's thesis for the doctorate. It is a service to all students of the history and philosophy of science to have this scholarly treatise available in English. The basic result is to show that it is in a real sense misleading to regard Hobbes solely as a materialist. "He is the philosopher of motion as Descartes is the philosopher of extension." Hobbes is "a philosopher of mechanism in a strict, unsurpassed sense."

OUR KNOWLEDGE OF THE EXTERNAL WORLD.

By Bertrand Russell.
W. W. Norton and Co., Inc.
$3.00 5½ x 8⅜; ix + 268 *New York*

The growing general interest in philosophy has called forth the republication of a number of really important philosophical books for popular consumption. Of current writers in English, Russell is probably the ablest in combining genuine philosophical authority with a clarity of statement intelligible to the non-professional reader. The reissue in editions of moderate cost of some of his early works by the W. W. Norton Company is therefore to be heartily welcomed. The present volume comprises the author's Lowell Lectures delivered in 1914 before the war turned Mr. Russell's attention to the consideration of problems of immediate social concern, and away from metaphysics, to the great loss, we think, of philosophy. They should be of interest to the thoughtful scientist, since they are concerned with the problem of understanding the physical world. But since the author deliberately defines the field of philosophical inquiry to exclude those particular problems which can be solved by the usual scientific procedures, the practicing investigator is not likely to get any immediate assistance. Russell attacks the intuitionist method of arriving at truth and supports an analytical procedure in philosophy as well as in physical science. For this, logic is indispensable, but the older syllogistic logic of Aristotle is inadequate, and an outline is given of the newer logistic or mathematical logic. Many of the ideas here popularly summarized have been elaborated in other later writings both by Russell and his co-worker Whitehead, the latter particularly in his *Science and the Modern World.*

LEIBNIZ.

By Herbert W. Carr. Little, Brown, and Co.
$3.00 5½ x 8½; vi + 222 *Boston*

In this, the first of a series of monographs on the philosophers who have mainly influenced Western thought, Professor Carr, after a brief sketch of the life and intellectual milieu of Leibniz, gives a more detailed discussion of his philosophical principles and of his influence on later generations. According to Carr's interpretation Leibniz was an important precursor both of the theory of relativity and of neo-vitalism.

THE COST OF BIOLOGICAL BOOKS IN 1929

By JOHN R. MINER

Institute for Biological Research, Johns Hopkins University

AT THE end of the first volume of The Quarterly Review of Biology (Vol. I, pp. 605–608, 1926) was inaugurated the plan of reporting annually on the cost of the books which had been received during the year. The present paper continues this plan with the report of book costs for the year 1929.

For the purpose of price comparison the books are classified by origin as follows:

I. *The United States.* Here are put all books published by strictly, or primarily, American publishers. Naturally the majority of books reviewed during the year have had this origin just as in earlier years.

II. *Germany.* In the number of books sent in by publishers for review, Germany stands next to this country.

III. *English-American.* In this group are placed the books which are manufactured and published in the first instance in England by publishing houses which have *branches* under their own name (not merely agents) in this country. The American branch imports the books into this country and distributes them here, priced in dollars rather than shillings.

IV. *England.* In this class are placed books published in England, priced in shillings, and available in this country only by direct importation, by the individual or through an agent.

V. *France.* This group includes all books published in France and her colonies.

VI. *Other Countries.* Here are placed all books published in any other country than those specified above.

VII. *United States Government.*

VIII. *British Government.*

Table 1 gives, for each of these eight rubrics, (*a*) the total number of pages in the books received for review; (*b*) the total cost of these books in dollars, foreign prices being converted to dollars on the basis of the exchange prevailing when the books were received; (*c*) the average price per page *in cents.*

TABLE 1

Prices of biological books, 1929

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
English-American	9,021	$171.40	1.90
Other countries	3,494	58.58	1.68
Germany	21,209	350.05	1.65
England	9,340	120.41	1.29
United States	79,710	905.39	1.14
France	11,371	53.66	0.47
British Government	392	1.54	0.39
U. S. Government	5,625	13.20	0.23

In order to facilitate comparison in respect of book prices, Table 2 has been prepared. In this table the following items are included: (*a*) the average price per page, in cents, for the years 1926–1929; (*b*) the absolute changes in average price per page, in cents, between 1926 and 1929, and between 1928 and 1929, a + sign denoting an *increase* in 1929 as compared with the earlier years, and a — sign denoting a *decrease;* (*c*) the percentage differences of the 1929 average price per page from those of 1926 and 1928, the + sign again indicating that the books were on the average higher in price in 1929 than they were in the earlier years, and the − sign that they were lower.

The first point to be noted from Table 1 is the continued increase in the total amount of book material noticed in The Quarterly Review of Biology. The total number of pages reviewed in 1929 is 140,162, an increase of 14.7 per cent over 1928, and of 69.7 per cent over 1926. The absolute increment of number of pages reviewed, which was almost constant in previous years, has decreased slightly in 1929. Apparently book material noticed is tending of its own accord towards an asymptote, but the amount of space available for book reviews may necessitate fixing a limit lower than this natural asymptote.

TABLE 2

Comparison of the prices of biological books from 1926 to 1929

ORIGIN	AVERAGE PRICE PER PAGE				CHANGE + OR − FROM 1926 TO 1929		CHANGE + OR − FROM 1928 TO 1929	
	1926	1927	1928	1929	Absolute	Relative	Absolute	Relative
	cents	*cents*	*cents*	*cents*	*cents*	*per cent*	*cents*	*per cent*
English-American	1.55	1.39	1.46	1.90	+0.35	+22.6	+0.44	+30.1
Other countries	1.51	0.78	1.13*	1.68	+0.17	+11.3	+0.55	+48.7
England	1.28	1.14	1.09	1.29	+0.01	+0.8	+0.20	+18.3
United States	1.12	1.09	1.14	1.14	+0.02	+1.8	0	0
Germany	1.09	1.20	1.48	1.65	+0.56	+51.4	+0.17	+11.5
British Government	—	0.96	1.26	0.39	−0.57†	−59.4†	−0.87	−69.0
France	0.35	0.36	0.45	0.47	+0.12	+34.3	+0.02	+4.4
U. S. Government	0.31	0.24	0.21	0.23	−0.08	−25.8	+0.02	+9.5

* With two special treatises omitted as explained in Vol. III, p. 601.

† Change from 1927 to 1929.

Turning to the prices given in Table 1 we find that the English-American books, which in 1926 and 1927 had been the most expensive but in 1928 had been slightly cheaper than the German books, again head the list. It should, however, be remembered that these prices include both transportation and the United States tariff, of 25 per cent ad valorem on books bound in leather, and of 15 per cent on those bound in other materials. For other groups the prices given refer to the country of publication and do not therefore include either of these charges.

As usual the biological books published by the United States Government stand at the bottom of the list, and next to them the British Government with one book on which the price was known. This is naturally too small a sample to be of much significance. France continues to produce the cheapest commercially published scientific books, costing on the average less than half as much as those of any other country.

As to the trends in prices shown in Table 2, England and the United States Government, which in previous years had shown a consistent decrease in price per page from year to year, in 1929 both show an increase. For English books this is large enough to bring the price slightly above the 1926 level, but the United States Government books, in spite of the increase, are still 25.8 per cent below 1926.

The German and French biological books, on the other hand, still show a steady rise in price per page. For our sample the German biological books were 11.5 per cent higher in 1929 than in 1928, and 51.4 per cent higher than in 1926. The corresponding percentage increases in the price of French biological books were 4.4 and 34.3 per cent. In the case of the French books the absolute price is so low that the percentage increase does not matter practically. For the German books, also, although they are among the highest priced on our list, there is one encouraging sign. The rate of increase in price of 1929 over 1928 is only half that of 1928 over 1927. Let us hope that German biological books are approaching a stable price level. There was no change in the price of biological books commercially published in the United States from 1928 to 1929 and only a slight increase over 1926 and 1927.

If all the books noticed in The Quarterly Review of Biology in 1929, regardless of origin, are lumped together and compared with all the books noticed in earlier years it works out that the average price per page in 1926 was 1.097 cents, 1.030 cents in 1927, 1.095 cents in 1928, omitting the two very expensive books noted, and 1.194 cents in 1929. This indicates an *increase* in average price of 9.0 per cent in 1929 as compared with 1928, and of 8.8 per cent as compared with 1926. On the whole it is obvious that, in the period reviewed, no violent price changes have occurred in either direction, if one envisages a generally balanced library of current biological books.

In concluding these notes for the present year, we should like again to emphasize that the statistical nature of the basic data is such as not to permit wide generalization. We are dealing here only with very small samples of books in general, and with by no means all of the strictly biological books. Indeed for some of the countries our samples are only fractions of the biological works there published. So the reader must be cautious in the kind of conclusions he draws from these annual reviews of the experience of The Quarterly Review of Biology regarding book prices.

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